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THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.

*Thesis approved for the Degree of Doctor of Science in the
University of London.*

By JAMES SMALL, D.Sc., Ph.C., F.L.S.

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THE ORIGIN AND DEVELOPMENT OF THE
COMPOSITÆ.

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PREFACE.

THE epilogistic nature of a preface is generally recognised, especially in the case of a reprinted serial such as this. I take the opportunity, therefore, of giving more precision to the number of species as mentioned in the Introduction. Since that was written a careful examination of the number of species and genera in the *Compositæ* which are upheld in the *Index Kewensis* and its *Supplements* up to 1910 has been completed, and has given the following figures. Total number of genera—997; genera not in the *Genera Plantarum* of Bentham and Hooker—199, of which 54 are old genera sunk in the original *Index* and resuscitated in the *Supplements*; 145 are new genera described since 1873. Total number of species—22,749, without including the genus *Hieracium*, of which it is estimated that about 6,000 microspecies have been described.

Several points have been revised or modified during publication. The most important is the production of new evidence for the trichome nature of the pappus (p. 284). Other points which may be indicated are the change in the position of the *Homochrominæ* to the position of basal sub-tribe of the *Astereæ* (p. 306), the change in the position of the *Eu-gnaphaliæ* to that of basal series in the *Gnaphaliinæ* (p. 302), the change in the derivation of the *Heleniæ* from the *Senecioneæ* instead of from the *Heliantheæ* (p. 312), and the various minor changes in the positions of some sub-tribes which are given in Chapter XIII.

Although a full index has not been provided it is hoped that the Detailed Table of Contents together with the Index to Genera (p. 327) may be a sufficient guide to the contents of the volume.

I would use this opportunity also to thank the many friends who have helped me with references to literature, material and criticisms; especially would I thank the Director of the Royal Botanic Gardens, Kew, the Regius Keeper of the Royal Botanic Garden, Edinburgh, and the Keeper of Botany, British Museum, for free access to living and herbarium specimens.

In his Hooker Lecture to the Linnean Society of London¹ Professor F. O. Bower, after giving an account of phylesis in the Filicales, said "The Angiosperms offer a still wider field; but it suffers from deficiencies of evidence, which have already been explained. What is urgently needed for success amid the multiplicity of their lines of progress is a widening of the bases of comparison. There must be a recognition of new criteria. A revision of the relative values of the old criteria will also be necessary." This account of the Compositæ is the outcome of a study of the family extending over about ten years. One of the most notable results is the opening up of the numerous lines of research which are indicated throughout the text, and in which I hope others will find the interest that leads to further research. In so far as success has been achieved in the unravelling of the tangled skein of the descent of this particularly large group of Angiosperms, it is due to the recognition of new criteria and the critical revision of the old criteria.

Apart, however, from any scientific progress which has been made in our knowledge of the Compositæ, the study of this wonderful group has become a labour of love, as it has always been with those who, like Berkhey, Cassini, Remy and Bentham, have attained an esoteric knowledge of the family of which J. J. Rousseau wrote—"On voit, dans les Composées, des métamorphoses et un enchaînement de merveilles qui tiennent tout esprit sain qui les observe dans une continuelle admiration."

September, 1919.

J. S.

¹ Jour. Linn. Soc., Bot., XLIV. 1918.

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THE ORIGIN AND DEVELOPMENT OF THE COMPOSITÆ.

BY JAMES SMALL, M.SC. (LOND.), PH.C.

INTRODUCTION.

THE present essay is an attempt to throw light on some of the problems of evolution by the intensive study of a single successful group. In 1874, when the section on Compositæ of Bentham and Hooker's *Genera Plantarum* (8) was published, the family included over 10,000 species; in 1897 when Hoffman completed the corresponding section of Engler and Prantl's *Pflanzenfamilien* (42) the number had risen to over 13,000; in the *Index Kewensis* and its supplements up to 1910 there are approximately 30,000 species in the family. In such a well-defined and closely inter-related family the genera tend to be founded on slighter differences than in other families and the species tend to become elementary or completely artificial rather than Linnean, so slight are the differences which are here considered to be sufficient for taxonomic purposes. In spite of this technicality the larger groups are more or less natural and the numerous intermediate forms between genera and tribes make the family a favourable subject for evolutionary studies.

The general habit varies so much with climatic and geographical situation that the vegetative characters are of little value in the study of the inter-relationships of the tribes, but there are cases where these features, added to well-marked floral relationships, confirm the lines of development already indicated. The physiology (irritability of the pollen-presentation mechanism, latex, etc.) and the cytology can be shown to develop in conjunction with the changes in floral structure, but ultimately the morphology of the flower and capitulum is the real test of relationship and development. The study of the details of the flower in this homogeneous group becomes, therefore, particularly important, and as there is least variation in the essential parts of the flower these must be considered

more important than the very variable non-essential parts. This was recognised by the first synantherologist, Cassini, and is confirmed by Bentham, the only other botanist who has studied the Compositæ sufficiently profoundly to express a sound and independent opinion.

After dealing with the history of the Compositæ we shall, therefore, consider the variation in the form and structure of the styles and stamens. As these are closely connected in the work of pollen-presentation the development of that mechanism, including its susceptibility to stimuli, is of first importance.

The variations in the corolla are considered in relation to the floral development and insect visitors; the variations in the pappus are considered in relation to the component parts of the trichome and the dispersal of the seeds. The characters of the receptacle and involucre are considered in relation to their development as indicated by closely allied forms of receptacle and involucre and in relation to the lines of evolution suggested by the examination of less variable parts of the capitulum. The various phylogenetic lines indicated by the critical examination of these floral characters are tested by the geographical distribution of the groups and the phyllotaxis and cytology of the family are found to follow the phylogenetic lines established by the preceding investigation.

In the discussion of the inter-relationships of the tribes and genera, use is made of the modern theories of heredity, evolution and geographical distribution. Some of these may be regarded as rather speculative, but their use is considered justified by the coherent account of the evolution of the family which results. Lines for further research are abundantly indicated and correction or confirmation of the views expressed will be sought along the various lines of physiological relationships, cytological and geological development and the details of geographical distribution.

CHAPTER I.

HISTORY OF THE CLASSIFICATION OF THE COMPOSITÆ.

IN the history of synantherology the classifications of the taxonomists have been in the majority of cases more or less artificial attempts at grouping related genera and only a few have made any attempt at expressing the affinities of the tribes and sub-tribes. On the other hand a number of students of the Compositæ have expressed views concerning the relationships of the tribes, but these views have been founded in some cases on somewhat limited enquiries into the anatomy and morphology of a number of genera.

It has been found convenient, therefore, to discuss the history of the grouping of the genera into tribes and the history of the grouping of the tribes according to their supposed relationships in separate sub-sections.

A. TAXONOMY.

The present sub-section deals not so much with the precise details of the classification of the family as with the evolution of the idea of the family as such and of the ideas of the different tribes as groups. It is an attempt to trace this evolution from the first more or less sub-conscious grouping of *Sonchus*, *Cichorium* and other Cichorieæ by Theophrastus to the modern conceptions of the divisions and sub-divisions of this immense and homogeneous mass of species.

Ancient Systems.

Theophrastus. Circa B.C. 320.

The origin of the idea of two of the tribes of the family, the Cichorieæ and Cynareæ, seems to be lost in antiquity like the origin of some other very natural groups, which, as Greene (37) says, must have been recognised by primitive man from the earliest times. They are distinguished very clearly by Theophrastus in his *Enquiry into Plants* (83). The chicory-like plants (κίχωριώδη) discussed in Book VII, Chapter XI, include *Cichorium*, *Hypochaeris*, *Taraxacum* and *Picris*, all described and distinguished from one another and given, moreover, only as examples of the class. The distinguishing characters of the group are given clearly and concisely. Theophrastus also mentions in Book I, Chapter X, the pine-thistle and "all the plants which belong to that class," the ἀκανθῶν or ἀκανθωδῶν. As he mentions the Acanaceæ again more than once it is obvious that the recognition of the Cynareæ as a group was to Theophrastus

a commonplace. In Book I, Chapter XIII, he also describes a group of plants distinguished by having the flower on the top of the actual seeds and with one flower attached to each seed; as these are described as "all thistle-like plants" it seems tolerably certain that in addition to Cichorieæ and Cynareæ this perspicacious Greek recognised the Compositæ as a class. The only other large obviously natural family which corresponds to this definition is the Umbelliferæ and this was separated as the Ferulaceæ.

Dioscorides. Circa A.D. 65.

According to Smith's Classical Dictionary, Pedacius Dioscorides probably lived in the second century A.D., but Burgess (16) gives evidence for a date about 65 A.D. for the writings of this author; Adanson (1) gives 50 A.D. as the date. The variations in the different editions of his *Materia Medica* are notorious but as early as 1555 the grouping of *Sonchus*, *Cichorium*, and *Chondrilla* by Dioscorides was amplified in the annotations of a Castilleian edition by Dr. Andrés de Laguna (23) who noted the similarity to the above-mentioned genera of *Scariola*, *Picris* and *Taraxacum*.

In the edition of 1598 by Bauhin of Matthioli's Dioscorides (24) other groupings of Composites are to be noticed, thus Lib. III, Cap. XIX, deals with *Leucantha*, identified as *Carduus Mariæ* by Bauhin and the subject of Cap. XXI is identified with *Carduus stellatus*. Chapter 109 of the same book deals with *Tussilago Farfara*, 110 and 111 with forms of *Artemisia* and 112 with *Ambrosia*; similarly *Anthemis*, *Parthenium* (= *Matricaria*) and *Bupthalmum* (*Bellis*, according to Bauhin) are dealt with in chapters 137-139. It is possible that this grouping of *Anthemis* and *Matricaria* forms the first indication of the Anthemideæ and this is rendered more probable by the development of the group by Brunfels.

16th Century.

Following upon Dioscorides comes a gap in the history of botany in general of about fifteen centuries. During the 16th century various commentators on Dioscorides, such as Brunfels (15), Valerius Cordus (20) and Fuchs (31) established and extended the Anthemideæ while retaining the Cichorieæ and Cynareæ. Lobel (60) extended these three groups and classed a few genera of the Astereæ together. Cæsalpino (17) was the first to group the Compositæ as a whole. His "Herbaceæ pluribus seminibus" are divided into the "Anthemideæ" and "Cichoraceæ aut Acanaceæ." The "Anthemideæ," however, include all the Composites not in the Cynareæ or Cichorieæ, while the Anthemideæ as recognised by the earlier writers is considerably obscured.

17th Century.

Bauhin (6) fails to recognise the *Compositæ* as a family but retained the groups previously recognised, *i.e.*, the *Cichoriæ*, *Cynaræ*, *Anthemideæ* and *Astereæ*, and in addition he classed several of the genera of the *Inuleæ* together. A decade later Gerard (33) advanced still further with a suggestion of the *Calenduleæ* as a group and the consolidation of the *Inuleæ* in addition to the groups of *Lobel*.

In the latter half of the century Morison (65) and Ray (72-73) again recognised the *Compositæ* as a family and agree in retaining the *Cichoriæ* and *Cynaræ* while confusing all the other tribes. The remaining authorities of the 17th century, such as Christopher Knaut (48), Rivini (75), Hermann (39) and Tournefort (84) agree in regarding the *Compositæ* as a family with the *Cichoriæ* as a distinct section, but confuse the other tribes. Knaut seems to be the first to use the name *Compositæ*, Ray's designation is "*Composito flore*." Hermann classes the group as "*Gymnomonospermæ Compositæ*."

18th Century.

The dominating systematist of this century, was, of course, Linné, but in his three attempts (59) at the classification of the *Compositæ* he made no progress whatever. Indeed, his first arrangement included so many external genera, such as *Globularia*, *Protea* and *Leucodendron* that he can scarcely be said to have recognised the family at all. His "*Syngenesia*" in the *Sexual System* include *Lobelia*, *Viola* and *Impatiens*! The *Ambrosia* group are separated for the first time in his *Natural System*.

Linné was preceded by a group of systematists whose ideas on the *Compositæ* varied very much. Boerhaave (12) gives the character "*staminibus propriis coalitis in tubum*" for the first time and has one section "*semine aculeis donato*" which foreshadows the *Heliantheæ*. Christian Knaut (49), Ruppius (76), Magnol (62), Ludwig (61), Allionius (2) and Necker (66) made attempts somewhat similar to the systems of Tournefort and Rivini; in some cases the presence or absence of rays was used as a diagnostic character.

The first botanist to consider the *Compositæ* alone was Vaillantus (85) whose system bears a distinct resemblance to that of Boerhaave, with an amplification of the *Heliantheæ*. Pontedera (71) gives a system very similar to that of his contemporary, Vaillantus, but with suggestions in his grouping of the genera of several tribes such as the *Senecioneæ*, *Calenduleæ*, *Astereæ* and *Heleniææ*, which were

not recognised by that systematist. Berkhey (9) and Meese (64) also published dissertations on the Compositæ but these show little or no originality.

Adanson (1) reviewed previous systems and places the Campanulaceæ next the Compositæ. He recognised some of the previously distinguished tribes (vide Table I) and followed Linné in separating the *Ambrosia* group but retained it within the family. Jussieu (46) makes the "antheræ connatæ" a diagnostic character of the family and foreshadows the Arctotideæ and Mutisieæ in his Cinarocephalæ anomalæ. In his arrangement of the genera Gaertner (32) follows Pontedera in the characters (receptacle, pappus and ray) used and arrives at a similar result, recognising the Inuleæ and Anthemideæ in addition to Pontedera's groups.

Early 19th Century.

In the beginning of this century Richard (74), Batsch (5) and Lagasca (51) followed their predecessors with little or no originality in the Compositæ, except that Richard used the divided or undivided style to characterise his two sections of the Synantheria.

Cassini, 1813-1834.

The founder of synantherology and the master in whose footsteps all subsequent students of the Compositæ have followed was Henri Cassini. As the result of a systematic analysis of all the floral characters he arranged the genera of the family into a series of 20 tribes with sections and sub-sections (vide 18, Vol. III, Synopsis) which have been retained as units during the various minor changes made by later systematists. There is no detail of morphology which escaped the notice of Cassini, and the present intensive study of the family by including physiology and geographical distribution can modify only slightly the grouping of the tribes. Even then Cassini had already indicated the existing relationships which will be emphasised later.

Cassinian Period, 1820-1917.

There have been three chief modifications of Cassini's system. Lessing (55) by using only the style characters reduced the number of tribes to eight but retained practically all Cassini's sub-tribes. De Candolle (21) followed Lessing with the addition of many original divisions of the sub-tribes. Bentham (8) returned to Cassini's system because he appreciated the value of the characters of the stamens and he acknowledges this return (7) but claims to have arranged the family before he was aware his system was so similar to that of Cassini.

The present system is, therefore, one reached independently by the only two botanists who ever studied the family sufficiently thoroughly to be able to speak with authority

Other systematists follow these four more or less closely: Bartling's system (4) is frankly Cassinian; Link (58) followed Cassini with several retrogressive variations; Lindley neglects Cassini and Lessing, returning to Jussieu (56) and later (57) following De Candolle. Endlicher (29), A. de Jussieu (47) and Eichler (27-28a) all follow De Candolle. Payer's arrangement (70) is a curious atavistic return to the early 18th century and Baillon (3) fuses several pairs of Benthamian tribes. Hoffmann's arrangement (42) shows no originality. One or two obvious sub-tribes are sunk and minor suggestions made by Bentham are carried out. Hoffmann gives an artificial sub-division of the Cichorieæ, but Engler and Gilg (30) returned to the Benthamian arrangement. Wettstein (89) follows Hoffmann.

Floras.

The Floras of any given period usually follow the current system. Thus Meese (63) and Nuttall (69) follow Linné; Kunth (50) follows Cassini with slight variations; Gray follows first De Candolle (34-35) and then Bentham (36). Boissier (13) follows Bentham.

American Systems.

The Americans show a tendency to raise the status of the groups: thus Jepson (45) raises the Ambrosinæ and Madinæ to the rank of tribes; Britton and Browne (14) raise the Ambrosinæ and Cichorieæ to the rank of families; J. K. Small (79) follows Britton and Browne, and Bessey (11) raises all the tribes and the Ambrosinæ to the rank of families, making fourteen in all.

Special Memoirs.

Don (25) and Schultz-Bipontinus (78) attempted classifications of the Cichorieæ. Nees (67) and Burgess (16) have dealt with the Asters and Delpino (22) proposed a new sub-division of the Senecionideæ of Lessing, but these isolated memoirs have had no effect on the general classification of the family.

Conclusion.

From Table I it will be obvious that the history of the classification of the Compositæ is clearly divided into two epochs, pre-Cassinian and Cassinian, with little or no advance from Theophrastus until the few decades immediately preceding Cassini, in which some slight indications are given of the origin of the ideas of a few of the tribes afterwards defined by the master. The half century

8 Tribes recognised before and after Cassini.

following Cassini was marked chiefly by the burying of his classic memoirs by Lessing and De Candolle and the present Benthamian period is nothing more than a return to the teaching of the greatest of all synantherologists.

TABLE I.
Tribes recognised from Theophrastus to 1915.

Date.	Author.	Compositæ.	Vernoniæ.	Eupatoriæ.	Asteræ.	Inulæ.	Helianthæ.	Heleniæ.	Anthemidæ.	Senecionæ.	Calendulæ.	Arctotidæ.	Mutisiæ.	Cynaræ.	Cichoriæ.
B.C.															
320	Theophrastus	+												+	+
A.D.															
65	Dioscorides								?					+	+
1532	Brunfels								+					+	+
1540	Cordus								+					+	+
1542	Fuchs								+					+	+
1570	Lobel				+				+					+	+
1583	Caesalpino	+							?					+	+
1623	Bauhin				+	?			+					+	+
1633	Gerard	?			+	+			+		?			+	+
1680	Morison	+							+					+	+
1682-86	Ray	+												+	+
1687	Knaut (1)	+												+	+
1690	Rivini	+												?	+
1690	Hermann	+												+	+
1700	Tournefort	+												+	+
1710-20	Boerhaave	+					?							+	+
1716	Knaut (2)	+												?	+
1718	Ruppius	+												+	+
1718-21	Vaillantus	+					+							+	+
1720	Pontedera	+			?		+	?		+	+			+	+
1720	Magnol	+												+	+
1737	Ludwig	+												+	?
1736-38	Linné	?												?	?
"	"	+					?							?	?
"	"	+ *												?	?
1757	Allionius	+												+	+
1760	Berkhey	+												+	+
1760-61	Meese	+					?			?				+	+
1763	Adanson	(+*)					+							+	+
1789	Jussieu	(+*)					+			+		?	?	+	+
1791	Gaertner	(+*)			+	?	+	+	+	?	?			+	+
1791	Necker	+					?		?					+	+
1801	Rich	+			?	?								+	+
1802	Batsch	+								+				+	+
1816	Lagasca	+					+			?				+	+
1818	Nuttall	+					?							?	?
1813-34	Cassini	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1820	Kunth	+	?	+	+	?	+		+	+			+	+	+
1829	Link	(+*)	+	+	+	?	+		+	+	?		+	+	+
1830	Bartling	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1832	Lessing	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1830-36	Lindley	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1836-38	De Candolle	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1836-40	Endlicher	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1860	Payer	+							+				+	+	+
1873	Bentham	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1875	Boissier	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1875-80	Biehler	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1882	Baillon	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1831	Gray	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1857	"	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1884	"	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1897	Hoffman	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1898	Britt. & Brown	+	+	+	+	+	+	+	+	+	+	+	+	+	+
1901	Wettstein	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1901	Jepson	(+*)	+	+	+	+	+	+	+	+	+	+	+	+	+
1903-13	Small, J. K.	+	+	+	+	+	+	+	+	+	+	+	+	+	+
1915	Bessey	+	+	+	+	+	+	+	+	+	+	+	+	+	+

+ Family or tribe recognised as a group.
+ * Ambrosiaceæ as a distinct family.
(+*) Ambrosiaceæ as a tribe or sub-tribe.

B. PHYLOGENY.

Beyond vague ideas of a common ancestry for some of the genera obviously very much alike, the pre-Cassinian writers on the Compositæ had apparently no thoughts of the evolution of one group from another within the family. It is, of course, well known that many of them were vehemently opposed to all evolutionary doctrines. As this question of creation or evolution is a general one and as Cassini was the first to distinguish the tribes sufficiently clearly to form any correct idea of their relationships the present account will be given in chronological order from Batsch and Cassini onwards. Another reason for the chronological order is that it emphasises the penetration of Cassini and the subsequent neglect of his valuable work by succeeding writers to the great detriment of synantherology.

Batsch, 1802.

In his *Tabula affinitatum* (5) Batsch discusses the affinities of each of his three groups of Composites. He considers the Lepid-*ocephalæ* (Cichoriæ) to be connected with the Cinarocephalæ (Cynareæ and Mutisieæ) through *Scolymus carduiformis* and *Barnadesia*, with the Campanulaceæ by the aggregation of the flowers and by the latex and with the Cucurbitaceæ by the bitter juice and disagreeable odour. The Cinarocephalæ he considers to be connected with the Valerianaceæ and Proteaceæ by the exalbuminous seed and aggregation of the flowers; similarly the Corymbiferae are said to have affinities with the Campanulaceæ.

Cassini, 1826.

The form chosen by Cassini for the expression of his views on the affinities of the tribes of the Compositæ is one seldom used but very useful. In Plate I of the *Opuscules* (18) he places the nineteen tribes each in a circle and the circles in an ellipse. Fig. 1 is from Cassini's diagram in the *Opuscules*, which he describes as a "tableau exprimant les affinités des tribus naturelles de la famille des Synanthérées." The Boopidées are the Calyceraceæ of modern systems. The interesting points in relation to the present study of the Compositæ are the affinities indicated between the Senecioneæ and the Eupatorieæ, the Senecioneæ and Astereæ, the Senecioneæ and Anthemideæ, the Senecioneæ and Mutisieæ, and between the Inuleæ and Cynareæ.

Lessing, 1832.

On page 425 of the *Synopsis* (55) Lessing gives a table of the tribes and sub-tribes of which he remarks "Analogiam subtribum singularum videre licet e tabula sequente." An examination of this arrangement (Table II) shows that Lessing followed Cassini in his

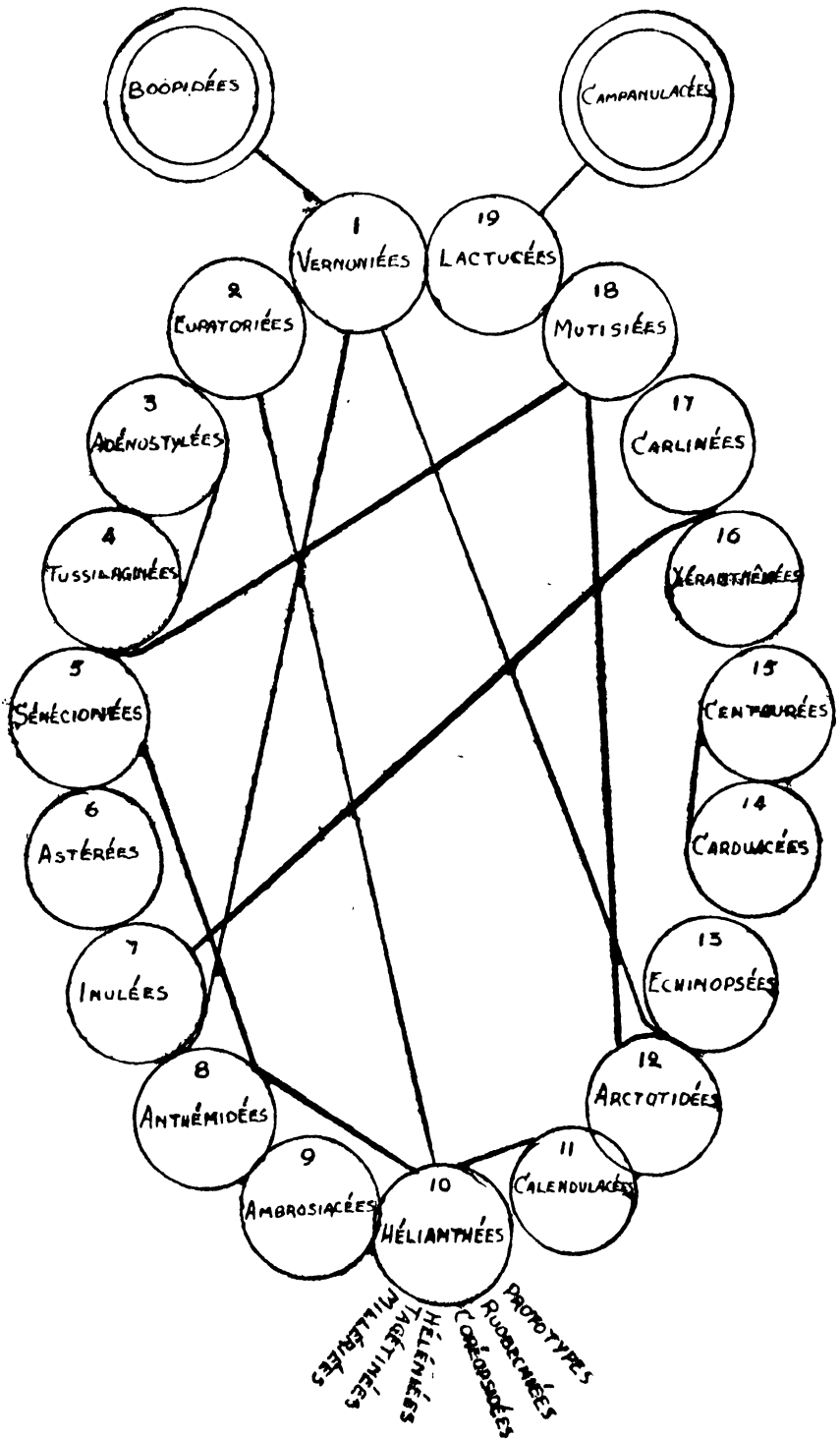


FIG. 1. Cassini's scheme of relationships of the tribes of Compositæ.

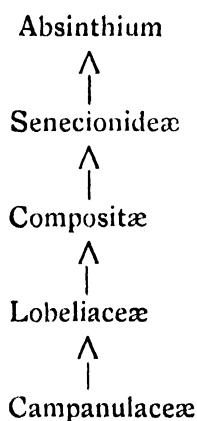
recognition of the affinities of the Senecioneæ with the Anthemideæ, Astereæ and Mutisieæ and that he correctly appreciated the similar affinities between the Senecioneæ, Calenduleæ and Arctotideæ. Hi

placing of the Othonneæ in the Cynaroideæ and the Tussilagineæ in the Eupatorieæ marks the affinity of the Benthamian Senecioneæ with these two tribes, as the Othonneæ and Tussilagineæ now form sub-tribes of the Senecioneæ. His grouping of the Inuleæ and Leyssereæ, Tarchonantheæ and Gnaphalieæ, Bupthalmeæ and Relhanieæ is interesting as all these are sub-tribes of the Inuloideæ of Bentham. Various other groupings are of minor interest but will be obvious to the synantherologist.

Delpino, 1871.

The stress laid upon the anemophily in *Artemisia* by Delpino (22) has been shown by Bentham (7) to have led to erroneous conclusions. His views on the origin of the family as shown in Table III are interesting on account of the recognition of the affinity between the Lobeliaceæ and Compositæ. It is necessary to remember however that his Senecionideæ is that of Lessing and includes the Heliantheæ, Helenieæ and Senecioneæ.

TABLE III. *Delpino's scheme of the derivation of Absinthium.*



Bentham, 1873.

Bentham followed Cassini very closely in his expression of the affinities of his tribes, as will be seen from Fig. 2, which is the arrangement given in Plate II. of the *Notes* (7). This diagram fails to indicate the close affinity of the Senecioneæ and the Eupatorieæ through the Tussilagineæ, recognised by Cassini and certainly not obliterated by the removal of that subtribe from the latter to the former tribe by Bentham. Similarly it omits the connection between the Cynareæ and Inuleæ noted by Cassini. It marks clearly, however, the affinities of the Senecioneæ with six other tribes.

In addition to the above diagram Bentham gave expression to other views on the history of the family in the text of the *Notes*

TABLE VI. *Analysis of Style-forms in the Compositæ.*

TRIBES AND SUB-TRIBES		TYPES.													
		1	2	3	4	5	6	7	8	8a	9	10	11	12	13
Vernonieae.															
Vernoniinae	..			30											
Lychnophorinae	..			13											
	Total			43											
Eupatorieae.															
Piqueriinae	..		8												
Ageratinae	..		23												
Adenostylinae	..		10												
	Total		41												
Astereae.															
Homochrominae	...			1½	½			5½	13	6½				1	1½
Grangeinae	..			½				3½	2½	½					½
Bellidinae	..				2			5½	2½	½					1½
Heterochrominae	...				3½			13	21½	4½					1
Conyzinae	..							6	4½						1
Baccharidinae	...							½	1½						1
	Total			2	6			34	44	12				1	6½
Inuleae.															
Tarchonanthoninae	...					1								1	1
Pluchinae	...				6									5½	6
Filagininae	..				4									6½	1
Gnaphalunae	..				32½	1								8	6½
Angianthinae	..				11									1	
Relbanunae	..				12									2	
Athrixinae	...				2½									4	½
Inulinae	...				2½									21½	
Bupththalmunae	...			½	6½									11	
	Total			½	77	2								60½	16
Hellantheae.															
Lagasceinae	..			1											
Millerinae	..							1	½						9½
Melampodinae	..														22
Ambrosinae	...					7									2
Petrobinae	..					2									
Zinninae	..			1	1			3							1
Verbesininae	..			2½	13½			25½	16					½	
Coleopsidinae	..			1	¼			7	8½						1
Galinsoginae	..				2½			4	2½						
Madunae	..			14				3							½
	Total			7	17½	9		44½	29½					½	36
Helenieae.															
Jaumeinae	...			1	2				1						
Baerinae	..			10		1		15½	7					½	
Flaverinae	..				3										
Tagetinae	..				6			4½	3½						
Heleninae	..				5½			1½	½						
	Total			1	26½	1		24½	12					½	
Anthemideae.															
Anthemidinae	..				14	1									
Chrysanthemidinae	..				31	1									
	Total				48	2									
Senecioneae.															
Liabinae	..				7										
Tussilaginatae	..		4					1							2
Senecioninae	..				19			5½	5½	1				2½	
Othonninae	..				5	2		1							
	Total		4	7	24	2		7½	5½	1				2½	2
Calenduleae					3										½
Arctotideae.															
Arctotidinae	...				1						7				
Gorteriae	...										1			5	2
Gundeliae	..										1			1	
	Total				1						9			6	2
Cynarae.															
Echinopsidinae	...											2			
Carlinae	..											1		7	
Carduinae	..											7½		10½	
Centaureinae	...											5		6	
	Total											15½		23½	
Mutisiae.															
Barnadesinae	..										2				
Onoseridinae	..				2			1½			6½				
Gochnatinae	..										13	1	1	7	
Gerberinae	..										8			2	
Nassauvinae	..				17						1				
	Total				19			1½			30½	1	1	9	
Cichorieae.															
Scolyminae	..		1												
Dendroseridinae	..		2												
Hyoseridinae	...		12												
Lapsaninae	..		3												
Rhagadiolinae	..		5												
Crepidinae	..		8												
Hieracinae	..		3												
Hypochaeridinae	...		8												
Lactucinae	...		14												
Scorzonerinae	...		13												
	Total		69												

latter. By reduction in the involucre and development of a setose pappus the Asteroideæ, Senecionideæ and Inuloideæ are said to have arisen in both Old and New Worlds from this Helianthoid plexus. Finally by a unilateral development of all the corollas, a reduction in the involucre and the development of a pappus he suggests the Cichorieæ arose also from the ancestral Helianthoideæ. It will be noticed that these opinions scarcely coincide with those expressed in the diagram (Fig. 2), and they will be discussed later in the light of the present investigation.

Vuillemin, 1884.

The most comprehensive study of the anatomy of the Compositæ is Vuillemin's *Tige des Composées* (86), an investigation "de la valeur des caractères anatomiques au point de vue la classification des végétaux." He concluded that although anatomical characters may be of value in the identification of fragments of plants such as drugs and fossil debris or in indicating the affinities of species within a genus or in special cases even genera within tribes, they were of no value as a basis for classification in the larger groups of the Compositæ.

Hildebrandt, 1887.

Vuillemin's conclusions were controverted three years later by Hildebrandt (40), who, however, confined his investigations to the Ambrosiaceæ and Senecionideæ (of Lessing). He reclassified the genera he examined on the anatomy of the stem, but his subsections as he characterises them show many variations in their anatomy, and there is an example of almost each type of structure in most of his subtribes.

Nichols, 1893.

After studying the achenial hairs of the Compositæ Nichols (68) decided that they were of no use as tribal characters. "Within the genus, however, the characters seem to be more constant, and might, perhaps, be made of value in the determination of species."

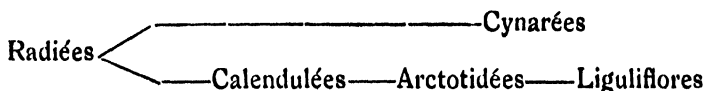
Höck, 1898.

Dealing with orders and not with families Höck (41) derives the Campanulatæ from a line showing epigyny; the main line gives a Rubialian line near the base from which a line leading to the Umbellifloræ is given off, the main line culminating in the Campanulatæ.

Col, 1899.

From his study of the laticiferous tissue and other secretory

canals in the Compositæ Col (19) considered that the Cynarææ had arisen from the "Radiées" and that the Calenduleæ, Arctotideæ and Cichorieæ were developed on a line of evolution parallel to that which gave the thistles. His views are expressed thus:—



Hallier, 1905.

The Campanulatæ according to Hallier (38) came from the Gymnosperms via the Polycarpicæ, Magnoliaceæ, Aristolochiaceæ and Passiflorales. He discusses briefly the Campanulacææ, Calyceraceæ and Compositæ, considering the last to be the highest expression of several of the tendencies shown by the Campanulatæ.

Lavialle, 1912.

After an elaborate and extensive investigation of the development and structure of the achene Lavialle (52) gave expression to an opinion upon the affinities of the Cichorieæ, Cynarææ and Mutisieæ. The examination included 298 species, 65 genera and most of the subtribes in the above-mentioned groups. Lavialle did not, however, extend his observations to the rest of the Compositæ so far as I have been able to ascertain at present. His views are given in the form of a diagram, Fig. 3, but their value is

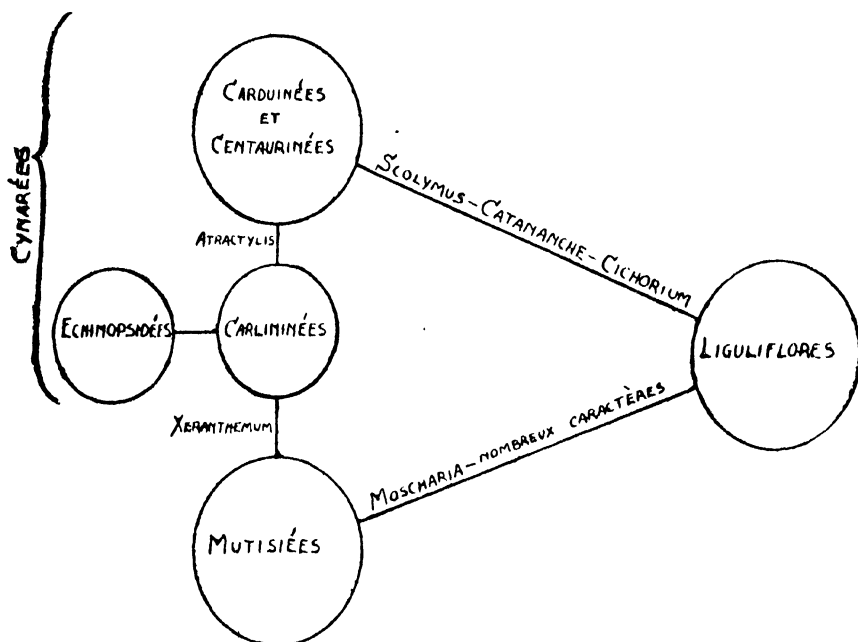


FIG. 3. Lavialle's scheme of the affinities of the Mutisieæ, Cynarææ, and Cichorieæ.

somewhat reduced by the limitation in the number of tribes examined.

Wernham, 1913,

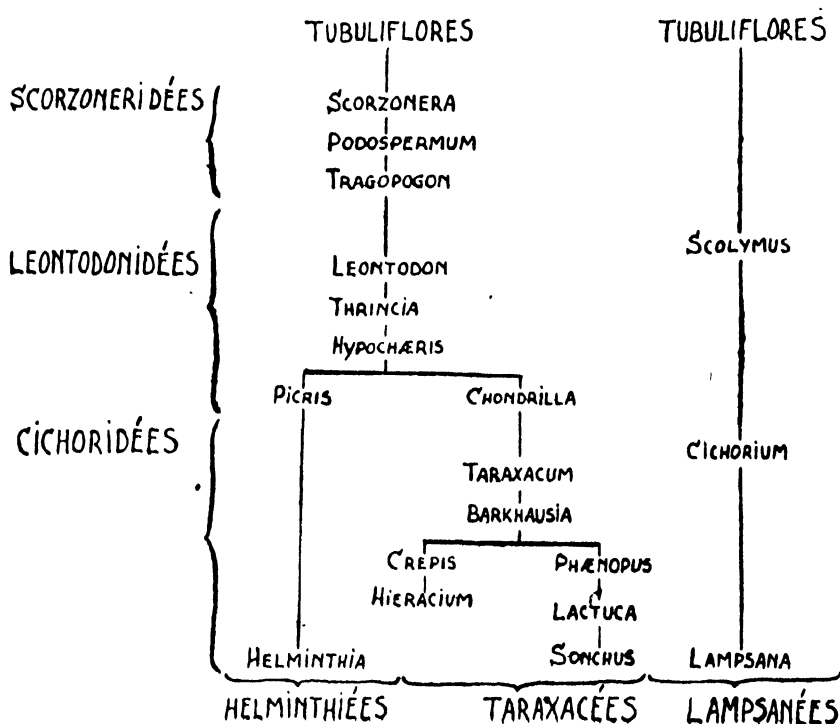
In his account of floral evolution in the Sympetalæ Wernham (88) does not consider groups below the rank of family but he supports the view that the Compositæ have arisen from the Campanulaceæ, an affinity which was recognised early in the history of the two families. The most important of Wernham's contributions is contained in the section on the determination of plant affinities in his "Summary and Conclusion" to which reference will be made later.

Dufour, 1907, and Lebard, 1913.

These two investigators (26 and 53) laid considerable stress upon the form of the cotyledons in the Cichorieæ, and Dufour proposed that the tribe should be divided on this character into two subtribes, the Brachycotylées (type *Lactuca* with short, broad cotyledons) and the Leptocotylées (type *Scorzonera* with long, narrow cotyledons). Dufour's work was carried further by Lebard, who distinguishes a form of cotyledon intermediate between the short and the long forms and gives a phylogenetic diagram shown in Table IV.

TABLE IV.

Lebard's phylogenetic scheme of the Cichorieæ.



He regards the Leptocotylées as primitive and the Brachycotylées as derived along two lines of evolution from the Tubulifloræ.

Lee, 1914.

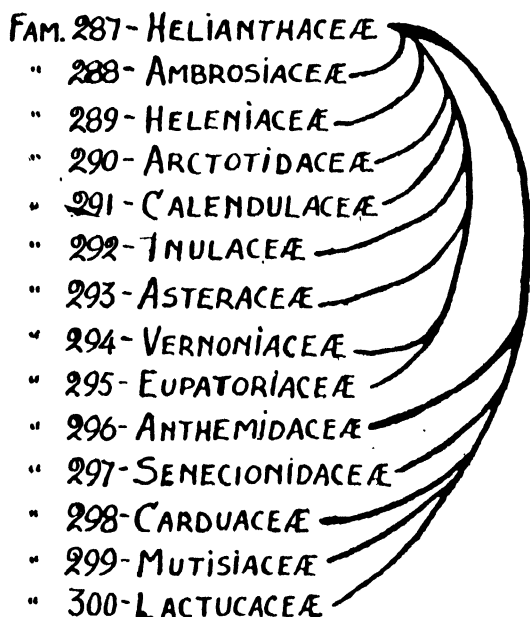
After an investigation of the seedling anatomy of about 50 species of Compositæ belonging to most of the tribes Lee (54) concluded that the classification in this family could receive no assistance from seedling anatomy. As he found all the types of anatomy which occur in the family in closely related species, and even in different specimens of the same species it is obvious that he was right in his conclusion that seedling anatomy is of no value in dealing with questions of affinity within the Compositæ. This is one more example of the failure of anatomy to give phylogenetic characters in the Compositæ, and agrees with the facts given by Vuillemin and Hildebrandt, although not with the latter's conclusions.

Bessey, 1897, 1915.

In his presidential address to the Botanical Society of America in 1897 (10) Bessey placed the Asterales at the summit of the Rubialian line of evolution. The four families included in the Asterales were supposed to be derived from one another thus:—Valerianaceæ—> Dipsaceæ—> Calyceraceæ—> Compositæ. The same author in 1915 (11) enunciated various dicta for determining

TABLE V.

Bessey's phyletic lines for the tribes of the Compositæ.



the phylogeny of flowering plants. These dicta, however, apply only to certain groups in each case. He raises the fourteen tribes of the Compositæ or Asterales to the rank of families, and regards the Helianthaceæ as the primitive group from which two principal phyletic lines have arisen, culminating in the Eupatoriaceæ on the one hand and the Lactucaceæ on the other. His views may be expressed as in Table V.

Hutchinson, 1916.

The Heliantheæ are also regarded as the most primitive tribe by Hutchinson (43) who considers the aristate or paleaceous pappus and the receptacular paleæ as primitive characters, and who also considers (44) the structure of the pappus in the Compositæ as "perhaps one of the most important features in the consideration of the phylogeny and affinities of the genera of this interesting family." This is very different from Bentham's view of both pappus and receptacular paleæ, the inconstancy of which in genera and sections led to that synantherologist to consider these characters as of use only when supplemented by other and more constant features.

Small, 1915-16.

The present writer has made various suggestions as to the affinities of the Compositæ and its constituent tribes. The first (80) was made after a study of the variation in styles and stamens and the elucidation of the function of the appendages of these organs. The chief point made was the establishment of similar lines of evolution from the consideration of the styles and of the stamens. As the work along these lines has been revised and extended it will be enough at this juncture to note that the Senecioneæ were considered the primitive group. In a subsequent study of the corolla (81) it was suggested that the Cichorieæ arose directly from the Senecioneæ by a comparatively small mutation. Other observations on the displacement and multiplication of the ovules in *Senecio vulgaris* (82) controverted the removal by Warming (87) of the Calyceraceæ from the neighbourhood of the Compositæ. These studies have been continued, and the present account is the result of the extended investigations.

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CHAPTER II.

THE POLLEN-PRESENTATION MECHANISM.

IN the Compositæ the mechanism involved in the presentation of pollen to the insect visitor includes both styles and stamens. These essential organs are discussed, therefore, in the present chapter, but for convenience the variation in structure of styles and stamens is described and discussed in separate sections, while their functions in the pollen-presenting mechanism is considered partly in section D of the present chapter and partly in Chapter III which deals with the irritability of the mechanism.

A. HISTORY.

The history of our acquaintance with the pollen-presentation mechanism may be divided into two distinct sub-sections, the first dealing with the development of our knowledge of the details of the essential organs and the second dealing similarly with the process of pollination.

Structure.

Pre-Cassinian Period.

Before the classic investigations of Malpighi and Grew there is no mention of either styles or stamens in the descriptions of Compositæ. Nehemiah Grew in his first book (29, 1671) describes the floret of the Compositæ as an "epitome of a flower." The anther tube and style are described and figured, and various secondary uses of these parts are given but the "Primary and Private Life I now determine not." In 1675 Malpighi (46) published good figures and descriptions of the styles and stamens in *Cichorium*, and in the following year Grew's fourth book appeared with numerous excellent figures and descriptions of the styles and stamens of several Composites. The Compositæ also furnish the basis of his chapter on "The Use of the Attire," a rather crude account of self-pollination in which both the style or blade" and the stamens or "sheath" are considered to be male organs, the "Thecæ of the Sheath" being described as the "Vegetable Sperme."

The first systematist to mention the characters of the styles and stamens as described by Malpighi and Grew was Vaillantus (70). Boerhaave in his first *Index* (7) did not give the distinguishing characteristics of his sub-divisions but did so in his *Index alter* (7). The syngenesious anthers and bifid stigma were now established as characteristic features of the family. Pontedera (56), distinguishes *Valeriana* by the stamens not being in a tube and also distinguishes other syngenesious forms, such as *Asclepius* and *Cucurbitaceæ* by their non-capitulate form, while Linné (43) uses the character as the primary one in his *Syngenesia* of the *Sexual System*. No further details of structure are given by subsequent authors (6, 25, 35, 59) up to the beginning of the Cassinian period.

Cassini (13) described the styles and stamens in great detail and used these details in his classification. Don subsequently used the basal appendages of the stamens in his classification of the *Cichorieæ* (20) and also records (21) abnormalities in several species of *Zinnia* with 4-10 stamens, 3-10 stigmas and 2-5 embryos. The styles and stamens were also used by Link (42), but his work is really of the pre-Cassinian type. Lessing (41) described the general staminal characters in great detail but used chiefly the stylar characters in his *Synopsis*, where he neglects the distinctive features of the stamens except in three tribes. De Candolle (17) used stylar characters for the tribes, but staminal characters for some of his sub-tribes, which were practically those of Cassini. The structure of the style was studied in great detail by Hildebrand (32) and by Chamberlain (14). The rudimentary stamens noted by the former in abnormal specimens were noted also by Cassini (13), Masters (48) and others.

Bentham (4,5) realised the importance of the details of both styles and stamens and used both for tribal and generic characters. Le Maout and Decaisne (40), Asa Gray (28) and other systematists agreed with Bentham and Cassini, while Baillon (2), using styles chiefly for his tribes, divided several of them into "sous-séries" on the anthers. The importance of the anther appendages in the biological efficiency of the pollen-presentation mechanism was emphasised by the present writer (61).

The development (9) and the vascular supply (30, 63, 67) of the styles and of the stamens (63, 67) and the structure of the pollen grain (3, 62, 71) have been described by various authors. Martin (47) considered that the tissue of the contiguous anthers

was in organic connection, while Coulter (15) and Merrell (49) report no such fusion. Observations by the writer prove that in some cases, at least, no organic connection exists, but the possibility of fusion in some species is not excluded and further research is in progress on this point.

Pollination.

Camerarius (10) was the first to conduct experiments in artificial pollination and to study pollination in the Compositæ. Miller (50) was the first to observe pollination by insects, but our knowledge of pollination in the Compositæ is founded on the later work of Kölreuter (38 and see Chap. III) and Sprengel (64). The latter noted the advantages of the capitulum and other characters in the Compositæ, and dealt with *Tussilago*, *Silybum*, *Centaurea*, etc. The next advance was about 40 years later when Brongniart (8) started a controversy on the function of the collecting hairs of the Campanulaceæ which led to a re-examination of the Compositæ for comparison by Hassall (31), Wilson (72), Todd (65) and Trelease (68). About this period also the study of pollination progressed rapidly under the stimulus of Müller's work (51), and the modern aspect of the subject together with the literature may be found in Knuth's compilation (36) based on Müller's contributions. The biology of *Helianthus annuus* and other Compositæ was the subject of several papers (12, 22, 27, 53), and Darwin (16) notes the sterile, pollen-presenting style which occurs in the male florets.

A valuable contribution was made by Juel (34) who distinguishes four chief types of pollen-presentation: (1) pollen presented on the tip of anther-tube, (2) pollen presented on the outer surface of the style and stigma, (3) pollen presented on the inner surface of the corolla lobes, (4) pollen presented directly from the anthers (anemophilous). Types 3 and 4 are comparatively rare, while type 1 is divided into two subsidiary types on the length of the male stage of anthesis, and type 2 has four forms, the *Gaillardia* type, the *Eupatorium* type, the Cichorieæ type and the *Arctotis* type, which differ in slight details.

The distribution of the sexes in the capitulum formed the basis of Linné's divisions of the Syngenesia, and this part of the subject has been studied exhaustively by Uexküll-Gyllenband (69) whose conclusions may be summarised as in Fig. 4 from her "Generalschema für die phylogenetische Blütenentwicklung." In

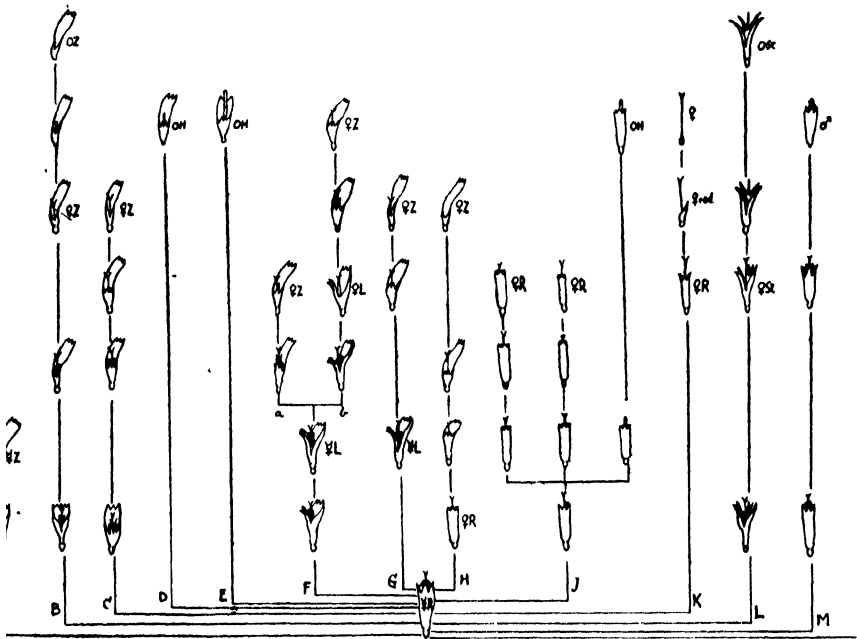


FIG. 4. Phylogeny of Flower forms (after Uexküll-Gyllenband).

A—*Hieracium barbatum*—Cichoriaceæ. B—*Anthemis Cotula*—Anthemideæ.
C—*Psadia glutinosa*—Asteraceæ. D—*Heterothalamus brunoides*—Asteraceæ. E—
Xeranthemum annuum—Cynareæ. F—*Gerbera* { a. *Wrightii* } Mutisieæ. G—
Anandria tomentosa—Mutisieæ. H—*Erigeron alpinus*—Asteraceæ. J—*Leontopodium*
alpinum—Inuleæ. K—*Haastia Sinclairi*—Asteraceæ. L—*Centaurea Jacea*—
Cynareæ. M—*Leontopodium alpinum*—Inuleæ. N—*Petasites albus*—Senecioneæ.

♂ R=hermaphrodite tubular floret. ♀ Z=hermaphrodite ligulate floret.
♀ L=hermaphrodite bilabiate floret. OZ=neutral ligulate floret. OH=neutral honey floret. OSt=neutral ray floret. ♀ Z=female ligulate floret. ♀ L=female bilabiate floret. ♀ R=female tubular floret. ♀ St=female ray floret. ♀ red.=female floret with reduced corolla. ♀ =female floret with no corolla. ♂ =male floret. Figures unmarked are intermediate forms occurring in the same capitula.

addition there have been many other studies of sex-distribution in the capitulum, such as 26, 33, 57 and 58.

Parthenogenesis and apogamy in the family have been studied by Murbeck (52), Ostenfeld (54-55), Schkorbatow (60) and others. The flowering period, which is usually autumnal in the north temperature regions, is the subject of notes by Bailey (1) and Lehard (39). Anemophily in the family is discussed at length by Delipino (18-19) and ornithophily in the Compositæ, Campanulaceæ and allied families is noted by Fries (24) and Trelease (68). The secretion of an intoxicating nectar in abnormal cases by *Centaurea Scabiosa*, *Carduus nutans*, *C. lanceolatus* and other species has been observed by Lloyd Williams (44).

The action of pollen grains mixed in various proportions from differently coloured capitula is the subject of a note by Lowe (45),

and the artificial germination of the pollen grains still presents difficulty. Ostenfeld (55) stated that "no one has been able to germinate the pollen grains of any Composite in artificial culture," but two years later Tokugawa (66) germinated the pollen of various Composites on the stigmas of plants belonging to other families, for instance the pollen of *Taraxacum albiflorus* and *Matricaria Chamomilla* germinated on the stigma of *Yucca gloriosa* and that of *Dahlia variabilis* on the stigma of *Abelmoschus Manihot* and *Hibiscus mutabilis*.

B. STYLES OF THE COMPOSITÆ.

The general type in the family is a slender style with two branches which are stigmatic on the inner surfaces. The style and style branches may be hairy or papillose or glabrous externally; style branches have appendages of various types, and the hairs of these appendages are arranged so that they either push or pull the pollen out of the anther tube; the stigmatic papillæ are conspicuous and arranged along the margins of the inner surfaces of the style branches, or they are less conspicuous and arranged either marginally or all over the inner surfaces. The vascular supply of the style is composed usually of two strands given off from a region of anastomoses at the top of the ovary; where the style is thick and practically undivided there are sometimes four vascular strands, as in *Arctotis* and *Tussilago* (63). The style in some genera is sensitive to touch (see Chap. III).

Types of Style.

The numerous variations can be reduced to fourteen types which will now be described.

Type I. Style branches slender, subterete or slightly flattened, papillose or glabrous externally; stigmatic papillæ all over inner surface from base to apex (Fig. 5, I).

Type II. Style branches elongated or short, subterete below, thickened and club-shaped or flattened and obtuse above, papillose or glabrous externally; stigmatic papillæ marginal and inconspicuous, confined to the lower part of the style branches. (Fig. 5, II and IIa). The upper sterile portions of the style branches are appendages.

Type III. Style branches elongated, subterete, subulate, more or less acute at the apex, hairy externally; stigmatic papillæ inconspicuous, extending in the centre of the inner surfaces of the style branches usually from the base to near the apex, but sometimes by

abortion of the upper stigmatic papillæ confined to the lower part of the style branches (Fig. 5, III).

Type IV. Style branches elongated or short, flattened, truncate at the apex, hairy or papillose externally; each branch ending in a brush of hairs considerably thicker and longer than those which clothe the outer surface; stigmatic papillæ in more or less conspicuous marginal lines, extending from the base to near the apex of the branches (Fig. 5, IV).

Type V. Style branches truncate and penicillate as in IV but with the inner surfaces permanently together (*i.e.*, the style branches do not diverge); stigmatic papillæ absent; very similar to IV before divergence of the style branches has taken place; characteristic sterile pollen-presenter in male florets (Fig. 5, V).

Type VI. Upper part of the style more or less swollen and hairy; style branches very short; stigmatic papillæ all over the inner surfaces of the style branches (Fig. 5, VI).

Type VII. Style branches elongated or short, flattened, each ending in a triangular appendage covered externally and internally with hairs which are usually longer near the base of the appendage; stigmatic papillæ in conspicuous marginal lines extending from the base of the style branches to the base of the appendages (Fig. 5, VII and VIIa).

Type VIII. Style branches as in VII, but appendages conical and more elongated (Fig. 5, VIII).

Type VIIla. Style branches as in VII, but stigmatic region short in comparison with the long, slender appendages (Fig. 5, VIIla).

Type IX. Upper part of style more or less swollen and hairy externally; style branches very short or practically absent; stigmatic papillæ all over inner surfaces (Fig. 5, IX).

Type X. Style branches very hairy externally, especially on the outside of the stigmatic part which ends in a collar of long hairs; style divided to the collar or more deeply; stigmatic papillæ all over inner surfaces of style branches above the collar (Fig. 5, X and Xa).

Type XI. Style as in X, but with the style branches remaining practically closed; stigmatic papillæ as in X but exposed only by a slight divergence of the style branches (Fig. 5, XI).

Type XII. Style branches elongated or short, flattened, hairy externally either from base to apex or only at apex, apex rounded; stigmatic papillæ inconspicuous, in two marginal lines which may

be narrow or so broad that only a narrow non-papillate region in the centre is left; very similar to IV, but distinguished by the rounded apex and frequently by the broader stigmatic lines (Fig. 5, XII and XIIa).

Type XIII. Style undivided, hairy externally, club-shaped, stigmatic papillæ absent; very similar to XII before the divergence of the style branches has taken place, characteristic sterile pollen-presenter of some male florets (Fig. 5, XIII).

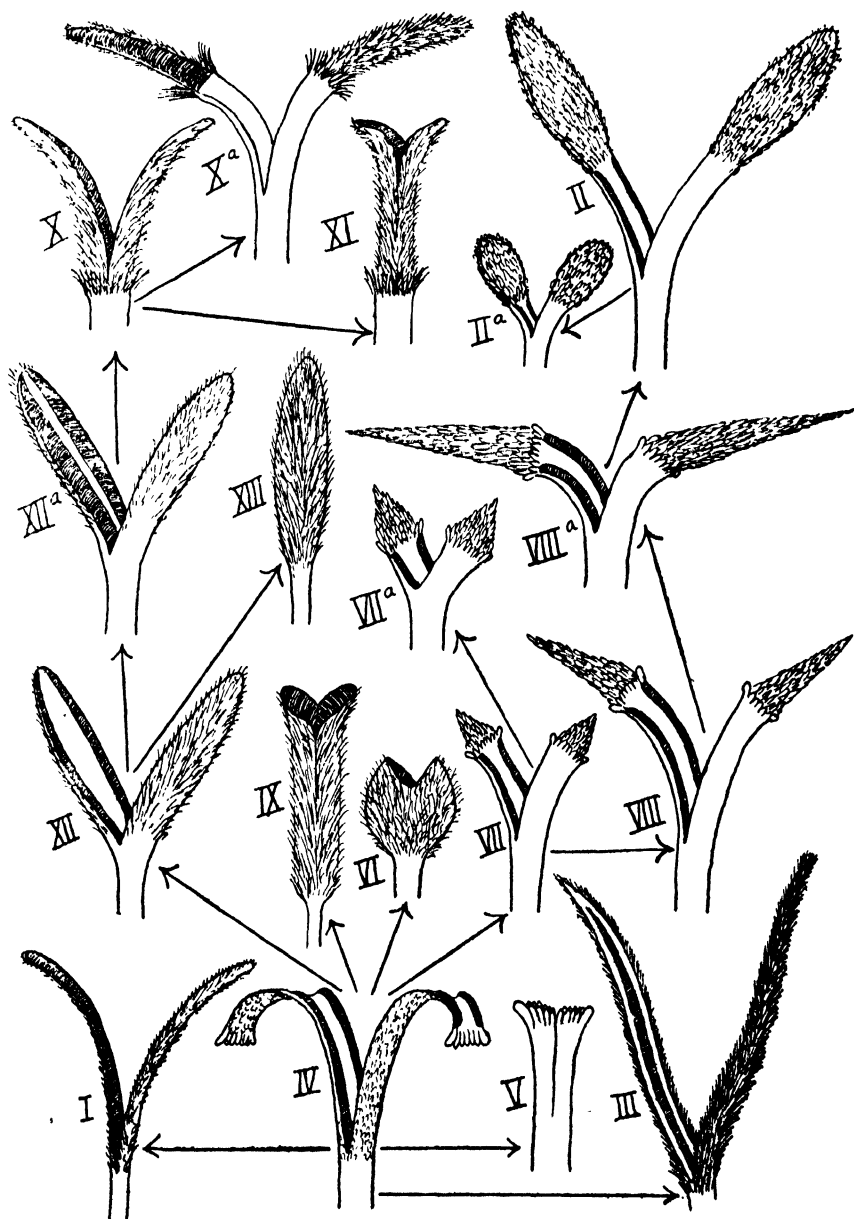


FIG. 5. Style forms in the Compositæ. The arrows indicate the lines of evolution.

Analysis of the Styles of Compositæ.

Analysis of the occurrence in the family of these various types of styles shows that type IV is the only one common to all except the more specialised tribes; it is, indeed, the typical style for the family, and the others are modifications of it. It will be obvious from the arrangement in Fig. 5 how type I has arisen from type IV by the disappearance of the truncate, penicillate apex and the elongation of the style branches. Type IV has also given rise to type V by the abortion of the stigmatic papillæ and the non-divergence of the style branches; to type III by the development of an awl-shaped apex and the transference of the stigmatic papillæ to the centre of the style branches; to types VI and IX by the spreading of the stigmatic papillæ and the partial fusion of the style branches; to type XII by the rounding of the tips of the style branches and the slight spreading of the stigmatic lines; and to type VII by the slight elongation of the hairy, apical part of the style branches (all stages of this change can be observed).

Types VII and XII then give two lines of development. Type VII by the shortening of the style branches gives VIIa; by the elongation of the apical appendages it gives VIII and then VIIla, which last by a flattening and thickening of the appendages gives II. Type II by a shortening of the style branches gives Ila. Type XII by the abortion of the stigmatic papillæ and fusion of the style branches gives XIII; by the spreading of the stigmatic lines it gives XIIa. Type XIIa by the further spreading of the stigmatic papillæ over the whole of the inner surface of the style branches and the development of a collar of long hairs gives type X, which by splitting more deeply gives Xa, and by partial fusion of the style branches gives type XI. Types V and XIII with no stigmatic papillæ occur in the male disc florets of some genera.

Having elucidated the probable evolution of the various style forms we can now analyse the composition of the tribes and sub-tribes of the family as regards their styles. In Table VI Bentham's classification is followed for reasons which will be obvious from the summary of the history of classification given in Chapter I, Section A. Engler's system of terminology is used, however, for the sake of uniformity. Various new genera are included, but the list is not quite complete.

The numbers are obtained by counting 1 for each genus in the sub-tribe which shows a given type of style. If the genus shows two types of style then it is counted $\frac{1}{2}$ in each of the proper

TABLE VI. *Analysis of Style-forms in the Compositæ.*

TRIBES AND SUB-TRIBES			TYPES.														
			1	2	3	4	5	6	7	8	8a	9	10	11	12	13	
Vernoniaeae.																	
Vernoniinae			30												
Lychnophorinae			13												
		Total			43												
Eupatoriaceae.																	
Piqueriinae		8													
Ageratinae		23													
Adenostylinae		10													
		Total		41													
Asteraceae.																	
Homochrominae			1½	1			5½	13	6½				1	1½	
Grangeinae			2				3½	1	2½					1½	
Bellidinae				3½			5½	2½	4½					1½	
Heterochrominae							13	21½						1	
Conyzinae							6	4½						1	
Baccharidinae							½	1½						1	
		Total			2	6			34	44	12				1	6½	
Inuleae.																	
Tarchoanthinae					1								1	1	
Pluchinae			6										5½	6	
Filagininae			4										6½	1	
Gnaphalinae			32½	1									8	6½	
Angianthinae			11										1		
Relbaninae			12										2		
Athrixinae			2½										4	½	
Inulinae			2½										21½		
Bupththalminae			6½										11	1	
		Total			½	77	2								60½	16	
Helliantheae.																	
Lagasceinae		1					1	½						9½	
Milleriinae														22	
Melampodiinae					7									2	
Ambrosiinae					2		1								
Petrobinae			1				3								
Zinninae			2½	13½			25½	16					½	1	
Verbesininae			1	½			7	8½						1	
Coreopsidinae				2½			4	2½							
Galinsoginae			1½				3	2						½	
Maduiniae			7	17½	9		44½	29½					½	36	
		Total			7	17½	9		44½	29½					½	36	
Helenieae.																	
Jaumeinae		1	2				3	1							
Baeriinae			10		1		15½	7					½		
Flaverinae			3												
Tagetinae			6				4½	3½							
Heleniinae			5½				1½	½							
		Total		1	26½	1			24½	12					½		
Anthemideae.																	
Anthemidinae			14	1											
Chrysanthemidinae			34	1											
		Total			48	2											
Senecioneae.																	
Liabinae		4	7				1							2	
Tussilaginatae			19				5½	5½	1				2½		
Senecioninae			5	2			1								
Othonninae		4	7	24	2		7½	5½	1				2½	2	
		Total		4	7	24	2		7½	5½	1				2½	2	
Calenduleae						3		5		½						½	
Arctotideae.																	
Arctotidinae			1							7					
Gorteriinae										1					
Gundelinae										1			5	2	
		Total			1							9			6	2	
Cynareae.																	
Echinopsidinae										2					
Carlininae										1			7		
Carduinae										7½			10½		
Centaureinae										5			6		
		Total										15½			23½		
Mutisiaeae.																	
Barnadesiinae										2					
Onoseridinae				2			1½			6½					
Gochnatiiinae										13		1		7	
Gerberinae										8				2	
Nassauviinae			17							1					
		Total			19				1½			30½	1	1	9		
Cichorieae.																	
Scolyminae		1													
Dendroseridinae		2													
Hyoseridinae		12													
Lapsaninae		3													
Rhagadioliinae		5													
Crepidinae		8													
Hieraciinae		3													
Hypochoeridinae		8													

columns. If, however, the genus shows three types of styles it is again counted $\frac{1}{2}$ in each column, and as it is only large genera which show three forms it is not altogether wrong to represent such a genus by a total of $1\frac{1}{2}$ in the table.

Type I is the characteristic style of the ordinary ray florets in all the tribes in which these occur and is noted in the table only in the Cichoriæ where it occurs without exception in every genus. It may be observed that the totals for the tribes do not quite agree with those given previously (61, p. 466), but further study has revealed differences, distinctions and intermediate forms unrecognised in the previous analysis.

The main points to be noted in Table VI are the following:—

Type IV is the only one which occurs in all except the specialised tribes;

Among the tribes in which type IV occurs the Astereæ, Helianthæ and Heleniæ are mainly types VII and VIII, so that they can scarcely be regarded as primitive in this respect; similarly the Inuleæ have many genera of type XII; the Arctotideæ and Mutisieæ have a considerable proportion of types IX and XII. This leaves the Anthemideæ, an obviously specialised group, and the Senecioneæ, which, while showing a large number of genera with type IV, has quite a number of other types, thus showing the characteristics of a primitive plexus, *i.e.*, a large percentage of primitive forms with an extended variability especially in the centre of the plexus (in this case the Senecioninæ), and a specialisation in the outer groups of the plexus (the Liabinæ and Tussilagininæ);

The occurrence of type III in the Senecioneæ and its exclusive predominance in the Liabinæ and Vernoniæ;

The monomodal curve of complexity, 6, 34, 44, 12, in the Astereæ and the passage of type VIIa of the Homochrominæ into type II of the Eupatorieæ;

The close relationship between types IV and XII and their occurrence in about equal numbers in the Inuleæ;

The similar close relationship between types IV and VII and their occurrence in about equal numbers in the Heleniæ;

The almost exclusive predominance of type IV in the Nasauviinæ.

These and other less obvious points will be discussed later in conjunction with others elucidated by the analysis of the stamens.

C. STAMENS OF THE COMPOSITÆ.

The stamens are five in number, and usually have the anthers syngenesious. As described by Cassini (13) the stamen is composed of the filament, which may be glabrous or hairy, the anther, the connective, the apical appendage, the basal appendages, the pollen and a prolongation of the connective below the anther to form the "article anthérifère." It is certain that in many species there is an abrupt change in the tissue of the stalk of the anther, but it is not always to be observed, and Bentham agrees with later authors in omitting it from his generic diagnoses. Cassini, however, was so impressed with this structure that he considered that the character of the family does not lie in the syngenesious anthers but in the "article anthérifère," and suggests (13, p. 139) that the family would be more appropriately known as the *Androtomæ* than as the *Synanthereæ*. This suggestion of alternative designations was Cassini's chief weakness as a botanist.

The apical appendage is practically always present, but the basal appendages may be absent, or may undergo modifications which have been used by Cassini, Bentham and others to characterise genera, sub-tribes or even tribes, and it is the form and degree of development of the basal appendages that give some clues as to the evolution of the family.

Types of Stamens.

The numerous varieties of stamens can be reduced to sixteen general types as follows:—

Type 1. Apical appendage absent; basal appendages absent; both base and apex of each anther lobe rounded and polliniferous (Fig. 6, 1).

Type 2. Apical appendage present, basal appendages absent; base of anther lobes truncate (Fig. 6, 2).

Type 3. Apical appendage present, basal appendages absent; base of anther lobes rounded and polliniferous (Fig. 6, 3).

Type 4. Apical appendage present; basal appendages very small, non-polliniferous auricles (Fig. 6, 4). In one genus, *Eleutheranthera*, this type occurs with the apical appendage absent as in Fig. 6, 4a.

Type 5. Apical appendage present; basal appendages more distinct as obtuse, non-polliniferous auricles (Fig. 6, 5).

Type 6. As type 5 but with basal appendages acute (Fig. 6, 6).

In a few cases the apical appendage is elongated as in 6a, in others the basal appendages are elongated as in 6b.

Type 7. As type 6, but with the auricles of contiguous anthers connate (Fig. 6, 7).

Type 8. Apical appendage present; basal appendages acute auricles, mucronate or prolonged into small tails (Fig. 6, 8).

Type 9. As type 8, but with the auricles and tails of contiguous anthers connate (Fig. 6, 9).

Type 10. Similar to type 8, but with longer tails (Fig. 6, 10).

Type 11. Apical appendage elongated; basal appendages acute, elongated auricles prolonged into tails (Fig. 6, 11).

Type 12. Similar to type 9, but with considerably longer tails (Fig. 6, 12).

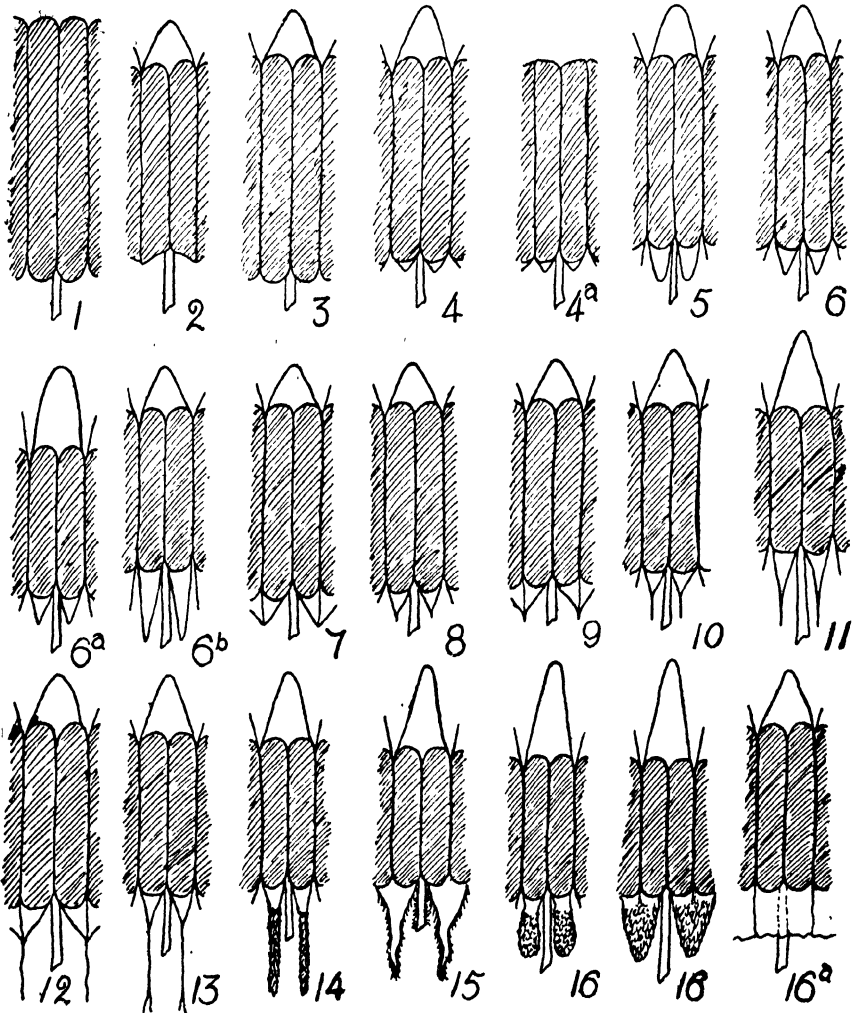


FIG. 6. Stamen forms in the Compositae.

Type 13. Apical appendage present; basal appendages acute; auricles with long tails divided into two or more filaments (Fig. 6, 13).

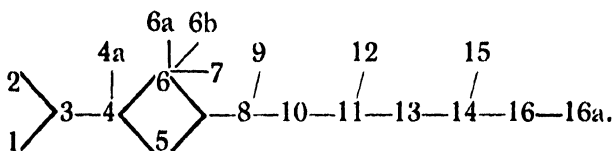
Type 14. Apical appendage elongated (oblong not triangular); basal appendages obtuse; auricles with long, flattened, lacerate tails (Fig. 6, 14).

Type 15. Similar to type 14, but apical appendage more elongated and tails of contiguous anthers connate (Fig. 6, 15).

Type 16. Apical appendage more elongated than in any other type; basal appendages flattened, elaborately lacerate tails, free or those of contiguous anthers connate (Fig. 6, 16). In one genus, *Tricholepis*, the fusion of the anther tails has been carried further, giving a continuous, membranous cylinder around the base of the anther tube (Fig. 6, 16a).

Analysis of the Stamens of Compositæ.

Analysis of the occurrence in the family of these various types of stamens show that type 1 is a special type occurring only in the specialised sub-tribe, *Piqueriinæ*, of the *Eupatoriæ*; type 2 is likewise a special form occurring in a few genera only, while type 3 occurs in a large number of genera belonging to eleven of the thirteen tribes. Type 4 also occurs in most of the tribes but is much less common than type 3, which is obviously the primitive and characteristic stamen for the family. Given type 3 as the basal form it is easy to see that types 1 and 2 are reduced forms while the others form a progressive series which may be given diagrammatically thus:—



Keeping this evolution of form in mind we can now analyse the composition of the tribes and sub-tribes of the family as regards their stamens in the same way as the styles have been analysed.

The main points to be noted in Table VII are the following:—

The primitive character of type 3, as already pointed out;

Type 3 occurs in all the tribes except the *Vernoniæ* and *Cynaræ*; it is predominant in the *Astereæ*, *Eupatoriæ*, *Anthemideæ* and *Senecionæ*;

Type 4 occurs in considerable proportion, with type 3 predominant in the *Helianthæ* and *Heleniæ*;

TABLE VII. *Analysis of Stamen-forms in the Compositæ.*

TRIBES & SUB-TRIBES.	TYPES.															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Vernonieæ.																
Vernoniinæ ...					18½	3	3			4½				1		
Lychnophorinæ ...					9½	2	½				1					
Total					28	5	3½			4½	1			1		
Eupatoriæ.																
Piqueriinæ ...	8															
Ageratinæ ...		2	21													
Adenostylinæ ...			10													
Total	8	2	31													
Asteræ.																
Homochrominæ ...		2	29													
Grangeinæ ...		2	4													
Bellidinæ ...			12½		½											
Heterochrominæ ...		2	37½	1						1						
Conyzinæ ...		1½	8½	1												
Baccharidinæ ...		½	2½													
Total	8	94	2	½						1						
Inuleæ.																
Tarhonanthinæ ...				1		1			1½	3½	½	3				
Plucheinæ ...						1				7		9½		1		
Filaginæ ...			1									3				
Gnaphalinæ ...			1½							44½		3	5½	1½		
Angianthinæ ...										7			3	2		
Rehmaninæ ...										6½		3	2½	2		
Athrixinæ ...										3½		1	2½			
Inulinæ ...										10		3	5	6		
Bupthalmînæ ...			1							9		6	3			
Total			3½	1		2			1½	91	½	31½	21½	12½		
Heliantheæ.																
Lagaceinæ ...			7	2½		1½										
Millerinæ ...			13½	7½												
Melampodiinæ ...	1		9		3											
Ambrosiinæ ...																
Petrobinæ ...			5½	½												
Zinninæ ...		5	29	23½	2											
Verbesinæ ...		1½	13	2½	1											
Coreopsidinæ ...		½	1	7	½											
Galinsoginæ ...		1½	5½													
Madinæ ...		9½	83½	43½	7½	1½										
Total																
Heleniæ.																
Jaumeinæ ...			5		2											
Baerinæ ...		1½	19	13½	1											
Flaverinæ ...			3													
Tagetinæ ...	1	11½	1½													
Heleninæ ...		2½	39	19½	3	2										
Total																
Anthemideæ.																
Anthemidinæ ...	1	12½	1½						1	1						
Chrysanthemidinæ ...	1½	33	2½													
Total	2½	45½	4													
Senecioneæ.																
Liabinæ ...		½	1	1	1	½		1	½		½					
Tussilagininæ ...			2	2			1½									
Senecioninæ ...		1½	21	8			½	1½								
Othonninae ...			6½	1½												
Total	2	30½	12½	1	1½	2	3½	½	1	3		1				
Calenduleæ.			3													
Arctotideæ.																
Arctotinæ ...		2		3½	2	1										
Gorteriinæ ...		1	2	1½				½		2						
Gundelinæ ...				2												
Total		3	2	7	3½	1	½			2						
Cynareæ.																
Echinopsidinæ ...									2			½			1	1
Carlhinæ ...									1½	1½		4		1	½	5
Carduinæ ...									2			3½		4½	1½	6
Centaureinæ ...									5½	1½		8		10½	13½	
Total																
Mutisiæ.																
Barnadesiinæ ...		1½	½								3½		6			
Onoseridinæ ...						1					6	1½	11	1½	1	
Gochnatiiinæ ...										1	3		½	5½		
Gerberinæ ...										1	11	½	1½	4		
Nassauviinæ ...										2	23½	2	2½	26½	1½	1
Total		1½	½		1											
Cichoreæ.																
Scolyminæ ...						1½		1								
Dendroseridinæ ...						5		6								
Hyoseridinæ ...			½		½	1½		1½								
Lapsaninæ ...						2½		2½								
Phagadiolinæ ...						4		4								
Crepidinæ ...						1		2								
Hieraciinæ ...						2½		4½								
Hypochaeridinæ ...						6		8								
Lactucinæ ...						6		7								
Scorzonerinæ ...						6		7								
Total			½		½	30		37								

A predominance of type 5 in the *Vernoniæ* is combined with a proportion of higher forms ;

A predominance of type 3 in the *Eupatoriæ* is combined with the occurrence of a few genera of type 2, and an exclusive predominance of type 1 in the *Piquerinæ* ;

A predominance of type 3 in the *Astereæ* is associated with a proportion of type 2 and a very few higher forms ;

The predominance of higher forms, types 10-14, in the *Inuleæ* and types 9-16 in the *Cynareæ* ;

The circumscribed variation in the types represented in the *Heliantheæ* (2-6), in the *Heleniæ* (2-6), in the *Anthemideæ* (2-4) and in the *Cichoriæ* (3, 5, 6, 8) ;

The considerable range of variation (3-16) in the *Mutisiæ* ;

The *Senecioneæ* again show the characteristics of a primitive plexus, but with the specialisation of the outer groups not shown as markedly as in the styles ;

The *Calenduleæ* and the *Arctotideæ* show a range of variation very similar to that of the *Senecioneæ* but without the predominance of type 3.

D. FUNCTION OF APPENDAGES OF STYLES AND STAMENS.

The biological significance of the hairs and appendages of the styles was appreciated by Cassini (13) and all subsequent authors, but the biological significance of the appendages of the stamens was elucidated for the first time in 1915 by the writer (61). Both Cassini and Bentham as shown above (Section A, Chap. II) recognised the value of these structures for the purposes of classification, but Cassini makes no mention of a possible function, while Bentham considers them to be "of little or no functional or homological importance."

That the predominant tendency in the *Compositæ* is economy has been emphasised (61-62), and "since the highest development of these appendages is found in the same groups with the greatest complexity in the structure of the style, it becomes highly probable that the appendages have quite a definite function" (61, p. 459). Economy in the polliniferous tissue was then considered and a new significance attached to the sweeping hairs of the styles and their efficiency in removing all the pollen grains from the anther tube. The main point can best be made clear by a quotation from the original article (61, p. 460). "The functions of the staminal appendages, hitherto obscure, become more obvious, for with the

corolla tube of a given length and the stamens in proportion, the amount of pollen produced can be reduced and the staminal tube remain the same length by the production of a membranous prolongation at the apex of each anther. This is a very simple method of reducing the polliniferous tissue while preserving efficiency of the staminal tube in the pollen-presentation mechanism. The function of the basal appendages is also made clear, since a tube terminating in ten more or less hemispherical lobes, as in type 3, could not be closed entirely by the style unless that organ actually entered the tube for some distance, in which case the pollen in that part of the sac past which the style had grown would be more or less lost for pollination purposes, unless it was swept up the tube by hairs situated lower down on the style. If the apex of the style merely reached to the lobes when the anthers dehisced, some of the pollen would fall through the interstices to the bottom of the corolla tube and thus be lost. If, however, the hemispherical lobes were prolonged into flattened auricles or ciliate tails or more elaborate appendages, the style, with or without appendages, could close the lower end of the staminal tube completely without encroaching on the polliniferous region, and thus no pollen would be wasted as far as the pollen-presentation mechanism was concerned."

From the further extended study of many forms there is no doubt that the above is the correct explanation of the variations in structure of the styles and stamens, and it is considered proved that these appendages and variations are the several modes of expression of a tendency in the Compositæ to economy of pollen, which is limited only by the biological necessity of providing sufficient pollen to ensure fertilisation.

Except in the relatively primitive groups, the Anthemideæ and Senecioneæ, relatively inefficient anther tubes are combined with efficient styles, as in the Eupatorieæ, Astereæ, Heliantheæ and Heleniæ, or relatively inefficient styles are combined with efficient anther tubes, as in the Vernoniæ, Inuleæ, Calenduleæ, Arctotideæ and Cichorieæ, or both styles and anther tubes are efficient, as in the Mutisieæ and Cynareæ.

Another point which is brought out by further study of the structure of the stamen is that Cassini's interpretation of the apical appendage and the "article anthérifère" as continuations of the connective is supported by the fact that the structure of these three parts of the stamen is very similar. This leads to the con-

clusion that both the apical appendage and the "article anthérifère," where it occurs, are produced by a contraction of the polliniferous region of the anther, *i.e.*, by a real sterilisation of potentially sporogenous tissue.

E. THE PHYLOGENETIC SIGNIFICANCE OF THE STYLES AND STAMENS.

As the complexity of the styles and that of the stamens have been shown to be more or less complementary, it is necessary in the elucidation of the phylogeny of the groups to consider, not so much the two sets of organs separately, as the complexity of the pollen-presentation mechanism as a whole. Each tribe will, therefore, be examined in order to determine the primitive and advanced sub-tribes and these will also be examined in order to determine their relations with one another throughout the family as far as it is possible to elucidate this from the pollen-presentation mechanism alone.

As the *Senecioneæ* appear from the analysis of both styles and stamens to be the primitive tribe it will be considered first. The *Liabinæ* are undoubtedly specialised in their style (Type III) but the types of stamens vary widely (2-9). The chief genus, *Liabum*, has comparatively simple stamens, type 2 or 6, and in the sub-tribe as a whole we get somewhat the same range of variation in the stamens as occurs in the *Vernoniæ*.

Three of the chief genera, *Homogyne*, *Cremanthodium*, *Alciope* and also *Luina*, in the *Tussilagininaæ*, show styles of type II. In *Luina* this is combined with stamens of types 8 or 10 and in *Alciope* with types 6 or 7, giving in both cases a relatively complex pollen-presentation mechanism. In *Homogyne* and *Cremanthodium* style type II occurs with stamens type 3 or 4, so that here the mechanism is less complex. Now *Cremanthodium*, although separated from *Senecio* as a distinct genus by Bentham and other systematists, is included in that genus by Franchet (23) who places it in the group *Ligularia* of *Senecio*, dividing that group into A-*Cremanthodium* and B-*Eu-ligularia*. It is really a mere matter of opinion, as even those who uphold the genus admit that it passes into the *Ligularia* group through such species as *Cremanthodium plantagineum*, Moor., which sometimes shows as many as five capitula instead of the solitary one which characterises the genus, and also through *Senecio calthæfolius*, Hk.f. (= *Cremanthodium Hookeri*, C.B.C.), which shows from one to four capitula. The only other distinction lies in the "nodding"

of the capitulum! The Tussilagininæ are, therefore, very intimately connected with the genus *Senecio*, which itself shows type VII styles not infrequently, and more rarely, as in some sub-sections of the *Ligularia* group, type VIII, thus leading up to type II in *Cremanthodium*.

The Othonninæ cannot be distinguished from the Senecioninæ by either styles or stamens, both being comparatively simple.

The Senecioninæ in both stamens and styles shows the characteristics of a primitive group. Type IV styles are combined in most genera with type 3 stamens, a simple and primitive pollen-presentation mechanism. *Senecio* itself, however, sometimes shows styles of types VII and VIII and sometimes stamens of types 4 or 8 but these two elaborations rarely, if ever, occur in the same species. They are, indeed, associated with two very different habits. Other closely allied genera always show type VII or type VIII in their styles, others always show type XII styles, which type also occurs in some species of *Senecio*.

It is not possible at this point to distinguish which is the more primitive of the two sub-tribes of the Vernoniæ but most of the large genera with simple stamens occur in the Vernoniinæ. *Vernonia* itself shows both type 5 and type 10.

In the Eupatoriæ the style is of a uniform type as in the Vernoniæ, so that the relative complexity of the pollen-presentation mechanism depends on the type of stamen. The simplest type of stamen occurs in the Piqueriinæ and nowhere else in the family. That this is a reduced, not a primitive type, is rendered probable by its occurrence only in this small and somewhat specialised group and is proved by the series of forms previously figured (61, Figs. 3-6). The normal apical appendage as in *Eupatorium cannabinum* (61, Fig. 6) becomes truncate and obviously reduced in *Sclerolepis* (61, Fig. 5) which is the genus in the Ageratinæ next the Piqueriinæ. In *Adenostemma viscosum* (61, Fig. 4) and other species of the chief genus in the Piqueriinæ the line of dehiscence does not extend to the apex of the anther when dehiscence is completed and the apical indehiscent region carries out the function of the ordinary apical appendage. In the other genera (61, Fig. 3) dehiscence is carried to the apex and the abortion of the apical appendage is complete. It is scarcely possible to distinguish at the present stage between the other two sub-tribes, but the complete uniformity in the stamens as in the styles of the Adenostylinæ indicates a probably specialised group.

The simplest pollen-presentation mechanism in the Astereæ is that of the Bellidinæ and Heterochrominæ, where stamens of type 3 are combined with styles of type VII in a number of genera. Styles of type VIII occur largely in the other sub-tribes and type VIIIa occurs in a notable percentage of the Homochrominæ, the sub-tribe placed next the Eupatoriæ by Bentham.

Considering next the Inuleæ, the Gnaphaliinæ is the only sub-tribe which shows a preponderance of simple (type IV) styles with a preponderance of comparatively simple stamens (type 10). The sub-tribe is divided into two series, the second of which, the Helichryseæ, has by much the larger proportion of simple type pollen-presentation mechanisms; the first series, the Eu-gnaphalieæ has a larger proportion of styles of type XII and of stamens of types 12 and 13. The other sub-tribes may be supposed to have come off as in Fig. 7, taking into consideration the predominance of type XII styles in the Inulinæ and Buphthalminæ, their development in the Athrixiinæ; the occurrence of simple stamens in the Plucheinæ and Filaginixæ with a considerable percentage of type XII styles; the occurrence of type V styles in the Tarchonanthinæ, and a larger proportion of type 10 stamens in the Angianthinæ than in the Relhaniinæ.

The largest proportion of simple pollen-presentation mechanisms in the Heliantheæ occurs in the Verbesininæ. Of the other sub-tribes the Lagasceinæ, Milleriinæ, Melampodiinæ, Ambrosiinæ and Petrobiinæ are obviously somewhat restricted or specialised, while the Zinniinæ, Coreopsidinæ and Madiinæ are closely allied to the Verbesininæ, but are on the whole higher in their style forms than the above-mentioned groups. The Galinsoginæ show a variation in the style forms more allied to that of the Heleniæ and are closely allied to but slightly higher than the Verbesininæ in their stamen forms.

In the Heleniæ a large proportion of higher type stamens is shown by the Jaumeinæ (type 5), the Baeriinæ (types 4-5) and the Heleriinæ (types 4 and 6). This is combined in the Jaumeinæ and Baeriinæ with a preponderance of higher type styles (types VII and VIII). The Flaveriinæ are obviously a specially simple group, while the Tagetinæ show a preponderance of simplicity with a range of variation which covers that of most of the other sub-tribes.

The Anthemideæ are a comparatively simple but special group, closely connected with the Senecioninæ and with practically no difference in the development of the pollen-presentation mechanism

in the two sub-tribes. The Calenduleæ are similarly closely connected with the Senecioninæ by their range of variation in both styles and stamens; the characteristic style of the tribe (type V) is easily derived from type IV.

The Arctotideæ show a considerable proportion of styles of type XII; the range of variation is very similar to that of the Senecioninæ and the stamens are considerably simpler than those of the majority of the Inuleæ, so that a derivation of the Arctotideæ from those genera (*Senecio* and *Erechthites*) in the Senecioneæ which show type XII styles seems more probable than one from the Inuleæ as suggested by the styles. Also *Ursinia* is the only genus in the tribe which shows a type IV style, and as it is one of the largest genera and shows type 3 stamens in addition, it seems to be another possible primitive genus in the group. Indeed, the tribe is markedly divided into two groups on the style. The occurrence of stamens of types 8 and 10 in the Gorteriinæ with type XII styles seems to indicate that this sub-tribe has arisen from the Inuleæ (from either the Plucheinæ or more probably the Gnaphalliinæ) and has then given rise to the more specialised Gundeliinæ. The Arctotidinæ seem to be more probably derived from the Senecioninæ through *Ursinia* with a IV-3 pollen-presentation mechanism. This is a point which requires other characters for its decision.

In the Cynareæ the Echinopsidinæ are obviously specialised, while the large percentage of advanced styles (type XI) and advanced stamens (type 16) in the Carlininæ and Carduinæ indicates that these are more advanced groups than the Centaureinæ, where there is a smaller percentage of type XI styles and where the stamens are generally type 12 or type 15.

The almost exclusive predominance of type IV styles in the Nassauviinæ clearly indicates an affinity for that sub-tribe with the Senecioneæ; the Onoseridinæ shows an affinity with the Nassauviinæ in the styles, while type 15 or 16 stamens are absent from both sub-tribes; the predominance of type 11 stamens in the Nassauviinæ makes the usual pollen-presentation mechanism of that group the simplest in the Mutisieæ. The Barnadesiinæ is a simple, special group, the usual combination being IX-3. The occurrence of styles of types X and XI and stamens of types 15 and 16 in the Gochnatiinæ places this group higher than the Gerberinæ, but as type XII styles are also present and as the stamens are of the higher types a possible affinity of these two sub-tribes with the Inuleæ is indicated,

It is very probable that most of the sub-tribes of the Cichoriæ are artificial, therefore it is not considered desirable to discuss their affinities. The derivation of type I styles from type IV has already been mentioned and as the stamens are of a relatively simple type a derivation of the Cichoriæ from the Senecioninæ is rendered probable.

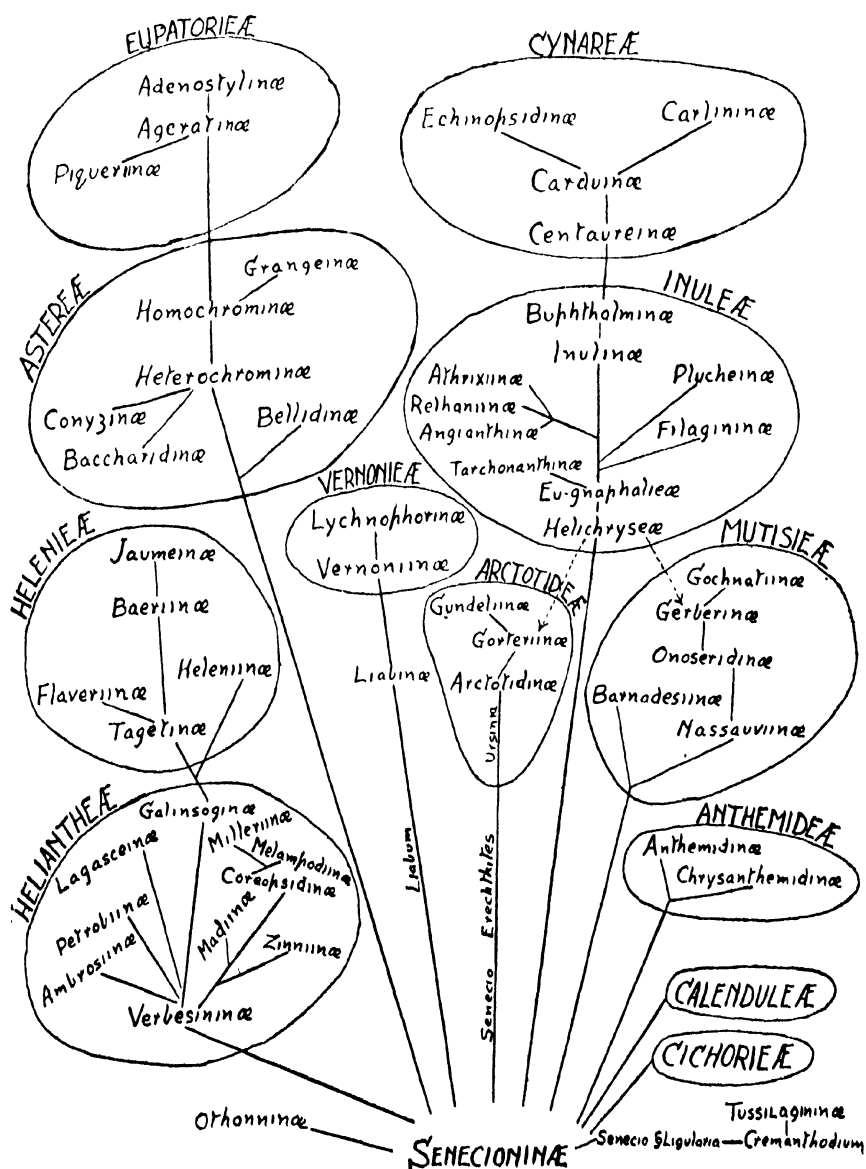


FIG. 7. Phyletic lines in the Compositæ as indicated by the Pollen presentation Mechanism.

All the affinities indicated by the preceding examination of the pollen-presentation mechanism of the various tribes and sub-tribes are shown in Fig. 7, including the somewhat problematical relationships between the Inuleæ and the Gorteriinæ and Gerberinæ, which may be no more than examples of parallel evolution.

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CHAPTER III.

IRRITABILITY OF THE POLLEN-PRESENTATION MECHANISM.

IT is probable that physiological differentiation precedes morphological differentiation in the history of a species and causal morphology must have a physiological basis for its sound study. Preliminary investigations are, therefore, in progress on the physiology of the Compositæ, and the present chapter deals with one of the most striking effects of physiological differentiation in the family, the irritability of the styles and stamens. The history of our knowledge of irritability is summarised briefly; the known cases of irritability are given, their physiology discussed, and the phylogenetic significance of the phenomenon in the Compositæ is considered in the light of the previous phyletic suggestions made in Chapter II.

A. HISTORY.

Styles :—Our knowledge of irritable styles in the Compositæ is of comparatively recent origin. The first reference to the movement of the style when touched is that in an unsigned article (30, 1815) by Ker on *Arctotis aspera*. He also records the same phenomenon in *A. aureola* (= *A. aspera*, L.), and suggests that "the style . . . seems to consist of a substance resembling elastic gum (Caoutchouc)."

Brown (4) refers only to Ker, and Cassini (7) records that he observed the phenomenon in "quelques arctotidées," but gives no details. Müller (43) and Knuth (34) give *Arctotis aspera* "and other species." Minden (42) records *Arctotis aspera* and *A. calendulacea* (= *Cryptostemma calendulacea*, R.Br.) as irritable, and discusses the physiology of the process (see below, Section D). Juel (28) extends the phenomenon to *Arctotis stoechadifolia*, and the writer has published a preliminary, illustrated account (47) of the phenomenon in *A. aspera*.

In other families the phenomenon of movement of the style or stigma when touched seems to have been known at a much earlier period, as the facts were apparently common knowledge when Kurt Sprengel (52, 1817) wrote of the irritable stigmas of

Mimulus and *Martynia* and the movements in *Scævola*, *Leeuwenhækia* and *Stylidium*. The movement in *Mimulus* is the subject of a note by Kitchener (33) and that in *Martynia* by Harger (21), while the physiology of the process in both genera and in *Strobilanthes* is considered by Oliver (44).

Stamens.:—The earliest record of the sensitiveness of the stamens in the Compositæ is that of Alexander Camerarius (5), who, while recording the phenomenon in *Cyanus Turcicus*, etc., quotes Borelli as having made the first observation on *Jacea aromatica*, the *Cardui pratenses*, the *Cyani* and *Stæbe*. Camerarius refers to the anther tube as the "vagina," but a few years later Bose (3) uses the term "stamina," and makes a passing reference to the irritability of these organs in some Compositæ. About half a century later Conte dal Covolo (10) discussed the phenomenon in *Centaurea calcitrapoides*, and gave very good figures of his detailed dissections. Previous to Koelreuter all recorded species except *Stæbe* (Inuleæ) belonged to the Cynareæ, but that author (36) extended the list to the Cichorieæ (*Hieracium*, *Cichorium*, *Scolymus*) and the Inuleæ (*Bupthalmum maritimum* = *Odontospermum maritimum* Sch. Bip.).

After the lapse of a century during which the only reference to the movement is a passing one by Cassini (7), the physiology of irritability was the subject of various investigations and discussions by Cohn (9), Unger (54-55), Hofmeister (24), Pfeffer (45) and others (see Section D). Hildebrand (23) added *Antennaria dioica*, and various Cynareæ were added to the list of "irritables" by Müller (43), Knuth (34), Meehan (40-41), Kirchner (32) and Linsbauer (37). Meehan (40) also records a peculiar irritability of the corolla in *Centaurea mexicana*, which, however, does not seem to have been confirmed. The trigger hairs on the filaments of some Cynareæ are described and figured by Kabsch (29), Unger (55), Kny (35), Haberlandt (15) and Halsted (16). The last (18) also extended the records of irritability to the Heliantheæ (*Echinacea*, *Heliopsis*)

Although he does not mention anything in the text Lubbock (38) extended the observations to the Anthemideæ. This is clear from his figures 87-88 of the anther tube in *Chrysanthemum parthenium*, in the first the tube is closed, erect, median and straight, in the second after an insect visit the tube is oblique, retracted and with the pollen exerted. Kerner and Oliver (31) mention *Onopordon* and *Centaureas* examples, and compare the mechanism with the

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mechanical action of the keel and style in some Papilionatæ. Juel, after a preliminary account, (27), extended the observations (28) to the Astereæ, Heleniæ, Senecioneæ, Arctotideæ, and Mutisieæ in addition to the Inuleæ, Heliantheæ, Anthemideæ, Cynareæ and Cichorieæ previously noted. The writer, after two preliminary notes (47-48), extended the list of "irritables" to 149 species and varieties (49), including the Calenduleæ and ten other tribes previously noted, but excluding the Vernoniæ and Eupatorieæ. Of the species observed 64% showed irritability.

Another type of movement is described by various authors, namely a gradual and automatic contraction of the anther tube. This is mentioned (25) and figured (26) by Jacquin for *Calea aspera*. Jacquin, however, considers the inclusion of the anthers to be due to an elongation of the corolla, and this is shown in his figure. Cassini (6) considered the inclusion to be due to the withering of the stamens, but Brown (4) described it as "a vital action, and not the effect of withering or decay, which, however, speedily follows it," and considered it to be analogous to the "more evident motion . . . in certain Cinarocephalæ." Another explanation was given by Meehan (41), who suggested that the filaments of *Helianthus* were stretched during exertion by the growth of the style against the closed, upper end of the anther tube, and that the subsequent retraction was due, not to irritability, but to the elasticity and spontaneous contraction of the filaments. Asa Gray (13-14) controverted this, and gave experiments proving that the style does not stretch the filaments, and that there is a lateral movement through 15 or 20 minutes of an arc when two adjacent filaments are touched, much as in the Cynareæ. Evans (11) has a note on a so-called unusual case of the re-exsertion of the style after the usual retraction of the style and stamens, but this is more or less usual, a typical case being *Arctotis aspera* as described by the writer (47, Fig. 1), who also found irritability of the ordinary type in a number of the Heliantheæ, the tribe of which this slow retraction of the anther tube is described as typical by Brown.

This movement, however, occurs in most tribes, and it seems probable that a confusion has occurred between the ordinary type of irritability and the retraction of the stamens due to the loss of turgor in the filaments which immediately precedes the withering of these slender structures. Thus Cassini was right if this loss of turgor is considered the first step in withering, Brown was right if the process of dying is considered to be a vital process, Meehan

is right in his explanation that the retraction is due to the elasticity of the filaments, and Gray is right when he controverts Meehan on the elongation of the filaments being due to a pressure exerted by the style. The proximate cause of the elongation of the filaments seems to be an increase in turgor (see Section D).

Irritable stamens in other families were unknown to the earlier botanists,¹ and according to Goeppert (12) the first to record the movement in *Berberis* was Linné (1775). Goeppert gives a good historical account up to his date (1828). Smith (51) was the first to locate a motor region in *Berberis*. Kurt Sprengel (52) recorded staminal movements in *Parnassia*, *Cacti*, etc.; Kitchener (33) recorded a gradual contraction and contortion of the filaments in *Achimenes*; Bessey (1), Meehan (39) and Halsted (17) made various observations on the movements of the stamens in *Portulaca* spp. Halsted also recorded experiments on *Berberis* (19-20). Tomney (53) records about 50 species of *Opuntia* which show irritability of the stamens, while Pfeffer (46) records the phenomenon in *Mahonia*, *Helianthemum* and other Cistaceæ, *Mesembryanthemum*, *Opuntia*, *Cereus*, *Sparmannia* and certain Tiliaceæ and Portulacaceæ.

B. IRRITABILITY OF THE STYLES.

Outside the Compositæ the only genus recorded as having a style which moves towards the touch is *Glossostigma* (46), but the stigmatic lobes are sensitive and close when touched in various other genera such as *Mimulus* (29, 33, 44, 46, 52), *Martynia* (Martyniaceæ) (21, 44, 46, 52), *Strobilanthes* (= *Goldfussia* Acanthaceæ) (44, 46) and *Bignonia* (Bignoniaceæ) (46). To these may be added *Torenia*. The stigma of *Torenia Fournieri* in India shows the same form of irritability as *Mimulus*, but other species, such as *Torenia vagans*, are not sensitive, nor is *T. Fournieri* when grown under glass in this country.²

In the Compositæ the phenomenon as at present known is confined to the Arctotideæ. It occurs in *Arctotis aspera* (30, 42, 47), *A. stoechadifolia* (28) and *Cryptostemma calendulacea* (28, 42). To these may be added the *Gazania splendens* of gardens. Ker (30) gives *Arctotis aureola*, Ker Gawl, also, but this is synonymous with *A. aspera*, L. The phenomenon in *Arctotis aspera* has been described in detail by the writer elsewhere (47), but a brief *resumé* is given below in order to facilitate reference.

¹ There is a considerable literature dealing with the stamens of *Berberis*, but most of it is irrelevant in the present argument.

² For this information about *Torenia* I am indebted to the Director of the Royal Botanic Gardens, Kew.

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Arctotis aspera, L.

The activities of the florets are best observed when the capitulum is examined on the plant in a green-house during warm, sunny weather. Anthesis begins about 8.30 a.m. in June; half an hour later the tips of some of the styles emerge from the anther tube and by 10 a.m. practically all the florets in the active whorl have their styles completely exerted; each style takes from five to ten minutes to emerge under the best conditions, and they are then sensitive to touch, bending from the base of the thickened portion towards the touch. The thickened portion is hairy and covered with pollen. When in a vigorous condition the style recovers its irritability in less than half a minute, but if touched so that it should react in an opposite direction from the previous movement two or three minutes rest are required in order to get a movement. This male stage of anthesis lasts for only one day in the case of the outermost three rows of hermaphrodite florets. The florets nearer the centre are male, and in these the style acts only as a pollen presenter, and may be withdrawn and exerted again in an irritable condition for two or even three successive evenings and mornings. The styles in these florets are not re-exserted after the male stage, but those of the outer rows of florets are exerted in the female condition with the short style branches spread apart on the second day of anthesis and remain exerted until the conclusion of anthesis. As a rule only one row of styles is in the irritable phase each day at the beginning of the anthesis of the capitulum and two or three in the later stages; there is a diurnal progression of maturity towards the centre of the capitulum.

Arctotis stoechadifolia, Berg.

This species (syn. *A. grandis*) shows a similar series of events, but the stamens are also irritable, so that by touching the anther tube when the style is first exerted one can observe a movement in one direction, while if the style is touched on the opposite side it moves in the opposite direction, or the style may be stimulated first and then the anther tube.

Gazania splendens, X.

This garden hybrid shows the same phenomenon as *A. stoechadifolia* but much more markedly. If the anther tube is touched gently after anthesis has begun the style is exerted with striking rapidity, being fully exerted (to the extent of about half an inch) within two minutes in favourable conditions of light and heat.

With the same touch the anther tube is stimulated to bend towards the touch, and this irritability remains during anthesis. The style is also irritable, and with the first touch after exertion moves as in *Arctotis*, but further touches have little or no effect for at least half an hour unless the same side of the style is touched, when a slight movement in the same direction as the first ensues.

The parents of *Gazania splendens* X are not known, but are said to be two of the three species—*G. ringens*, Gærtn., *G. pavonia*, R.Br. and *G. uniflora*, Sims.

It is noteworthy that all these three genera belong to the Arctotideæ, while three of the genera (*Mimulus*, *Torenia* and *Glossostigma*) in the other families belong to the Gratiolæ of the Scrophulariaceæ, and that these other families themselves all belong to Sections D and E of the Tubifloræ (Engler). The phenomenon seems to be restricted to a few narrow circles of affinities, and is not wide spread as in the case of irritability of the stamens.

C. IRRITABILITY OF THE STAMENS.

The basis of the present section is the following list, Table VIII, (pp. 53-59) of the species on the irritability or non-irritability of which observations have been made. The tribes are arranged according to their origin as shown by the structure of the pollen-presentation mechanism, and the sub-tribes are those of Bentham revised as before. The recognised affinities of the genera are indicated roughly by the numbers, which are those of the Genera Plantarum, except in cases where Bentham sunk a genus which is now upheld, e.g., *Leptosyne*, when a letter is added to the Genera Plantarum number of the containing genus.

Previous authors have not as a rule recorded the exact type of irritability, and those species not observed in the present investigation are indicated thus:—

(Cov) = irritability of the stamens recorded by Covolo;

(K) = " " " " Koelreuter;

(Kb) = " " " " Kabsch;

(Kn) = " " " " Knuth;

(H) = " " " " Haberlandt;

(M) = " " " " Meehan;

(L) = " " " " Linsbauer;

(U) = " " " " Unger;

(J) = " " " " Juel;

(OJ) = absence of irritability recorded by Juel.

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The majority of the species have been examined by the writer and the types of irritability are distinguished thus :—

Types of irritability :

A : pollen presented on touching ; no lateral movement of the anther tube,

B : pollen presented on touching ; lateral movement indefinite in direction,

C : pollen presented on touching ; lateral movement towards the touch,

C' : pollen presented on touching ; lateral movement towards the centre of the capitulum,

C^e : pollen presented on touching with more or less explosive rapidity,

Q : no irritability observed when touched.

The degree of irritability is noted as slight when it requires careful observation, and various other degrees are noted. Various precautions are necessary for the successful observation of the phenomenon, for it was not without reason that Camerarius remarked of the observation of the movement that “*Verum enimvero patientia.*” The general method used in the present investigation was to examine the flowers on a hot, sunny day just after anthesis had commenced, and before an insect had visited the floret, by touching the filaments or anther tube gently with the point of a needle, and by observing the effect with the aid of a watchmaker's eyeglass. The latter was found very convenient as it left both hands free for manipulation. For the details of the precautions readers are referred to the previous paper (49).

The list includes 360 species and varieties, 253 or 70% of which show irritability ; all the tribes in the family are represented and 45 of the 64 subtribes, so that the list is sufficiently representative to form the basis of some phylogenetic suggestions.

NOTES ON TABLE VIII.

1. In all these cases (*Tussilagininae*) the critical stage, with the anther tube open and the style not completely exerted, is very short.

2. In *Doronicum Pardalianches* the style has frequently been observed to be bent by pressure against the top of the anther tube.

3. *Cineraria Moorei* is a garden hybrid between *C. Héritieri* and a form of *C. cruentes*.

4. *Cineraria stellata* is a florists' variety obtained from Messrs. Dobbie and Sons.

TABLE VIII.

Tribe and Sub-tribe.	Genus and Species.	Type of Irritability.	Remarks.
SENECIONEÆ.			
2 Tussilagininzæ	559 Tussilago Farfara, L.	O	(1)
	560 Petasites albus, Gaert.	O	(1)
3 Senecioninzæ	" officinalis, Moench.	O	(1)
	564 Arnica alpina, Olin & Ladau.	B	distinct
	" Chamissonis, Less.	O	
	" latifolia, Bongard.	O	
	" longifolia, Eaton.	O	
	565 Doronicum Pardalianches, L.	C	distinct (2)
	" plantagineum, L.	C	slow
	581 Gynura aurantiaca, D.C.	O	
	582 Cineraria Moorei, (Hort.)	O	(3)
	" stellata, (Hort.)	A	slight (4)
	583 Emilia sonchifolia, D.C.	O	
	585 Senecio adonidifolius, Loisel.	C	distinct
	" alpestris, D.C.	O	
	" aquaticus, Hill.	A: B	A distinct, B slight and slow
	" bellidioides, Hk.f.	C	distinct
	" Blumeri, Greene.	O	
	" clivorum, Maxim.	O	(5)
	" erucifolius, L.	O	
	" grandifolius, Less.	O	(6)
	" Grisebachii, Baker.	O	
	" hortensis, (Hort.)	C	clear (7)
	" Jacobaea, L.	C	A distinct, C slight
	" japonica, Sch.Bip.	C	slight
	" Ledebouri, Sch.Bip.	A	slight
	" Ligularia, Hk.f.	A	very slight
	" " var. speciosa.	C	very slow
	" palustris, Hook.	C	distinct
	" populifolius, D.C.	C	marked (8)
	" pulvinatus, (Hort.)	A	slight
	" sarracenicus, L.	(J)	
	" squalidus, L.	C	distinct
	" suaveolens, Ell.	(J)	
	" tropaeolifolius, MacOwan	C	distinct
	" turkestanicus, C.Winkl.	O	
	" viscosus, L.	A: C	A distinct, C slight but variable
	" vulgaris, L.	C	distinct (9)
4 Othonninzæ	589 Othonnopsis cheirifolia, Benth. and Hook.	A	slight
	592 Euryops pectinatus, Cass.	O	
	595 Othonna carnosa, Less.	C	distinct
CICHORIEÆ.			
1 Scolyminzæ	711 Scolymus hispanicus, L.	(K)	
3 Hyoseridinzæ	714 Catananche cærulea, L.	C	very marked (10)
	" " var. alba	C	"
	717 Cichorium 'Endivia, L.	C	slow (10)
	" Intybus, L.	C	distinct (10)
	723 Tolpis barbata, Gaert.	(OJ)	
4 Lapsaninzæ	725 Lapsana communis, L.	C	marked (11)
6 Crepidinzæ	735 Crepis biennis, L.	O	
	" blattaroides, Vill.	A	distinct (10)
	" virens, L.	C	distinct (10)
7 Hieraciinzæ	738 Hieracium balkanum, Uechtr.	O	

TABLE VIII (continued)

Tribe and Sub-tribe.	Genus and Species.	Types of Irritability.	Remarks.
7 Hieraciinæ(ctd)	738 Hieracium Bornmuelleri, Freyn.	O	
	„ bupleuroides, Gmel.	O	
	„ Gouani, Hegetsch.	O	
	„ grandifolium, Sch. Bip.	C	slight and slow
	„ maculatum, Schrank.	C	„
	„ murorum, L.	C	slight (10)
	„ pallidum, Biv.	C	very slight (10)
	„ Pilosella, L.	O	
	„ prenanthoides, L.	O	
	„ rubrum, Peter.	O	
	„ sabaudum, L.	(K)	
	„ tridentatum, Fries.	O	
8 Hypochæridinæ	742 Hypochæris radicata, L.	C	marked (10)
	„ „ var. hispida, Peterman	C	„
	743 Leontodon asperrimus, Boiss.	C	distinct (10)
	„ hirtus, L.	C	„
	„ hispidus, L.	O	„
9 Lactucinæ	745 Taraxacum officinale, Weber.	C	distinct (12)
	750 Lactuca Bourgæi, (=Mulgedium Bourgæi, Boiss.)	C	distinct (10)
	750 Lactuca bracteata, Hk.f.	C	very clear
	„ hastata, DC.	C	distinct
	„ perennis, L.	C	slight
	„ Plumieri, Gren. & Godr.	C	distinct
	„ virosa, L.	C	„
	755 Sonchus arvensis, L.	O	
	„ asper, Hill	C	distinct (10)
	„ oleraceus, L.	C	slight but distinct
10 Scorzonerinæ	760 Tragopogon orientalis, L.	C	distinct
	761 Urospermum Dalechampii, F. W. Schmidt	O	
	762 Scorzonera hispanica, L.	C	very slow but very distinct
	„ purpurea, L.	C	distinct
CALENDULÆ	597 Dimorphotheca aurantiaca, DC	C	very clear
	„ Ecklonis, DC.	C	marked (13)
	„ pluvialis, Moench.	C	distinct
	598 Calendula arvensis, L.	O	
	„ officinalis, L.	A	slight (14)
ARCTOTIDEÆ			
1 Arctotidinæ	604 Ursinia anthemoides, Gaert.	(J)	
	„ cakilefolia, DC.	A	distinct
	„ pulchra, N.E.Br.	C	variable (15)
	„ speciosa, DC.	B	„
	609 Cryptostemma calendulacea, R.Br.	(OJ)	
	610 Arctotis stoechadifolia, Berg.	C	distinct (16)
2 Gorteriinæ	613 Gazania rigens, Moench.	(OJ)	
	„ splendens, X.	C	distinct (16)
	616 Berkheya purpurea, B. & Hk.f.	O	
ANTHEMIDEÆ			
1 Anthemidinæ	515 Anacyclus officinarum, Heyne	C	distinct
	516 Achillea alpina, L.	C	slight
	„ Clavennæ, L.	C	slight
	„ crustata, Schur.	A	marked
	„ grandiflora, Bieb.	C	marked

TABLE VIII (continued)

Tribe and Sub-tribe.	Genus and Species.	Types of Irritability.	Remarks.
ANTHEMIDEÆ(OLD)			
1 Anthemidinæ (continued)	516 <i>Achillea holosericea</i> , Sibth. and Sm. „ <i>macedonica</i> , Rouy. „ <i>magna</i> , L. „ <i>Millefolium</i> , L. „ <i>nobilis</i> , L. „ <i>obscura</i> X, Nees. „ <i>Parmica</i> , L.	A O C C O O C	slight (17) distinct marked distinct (18)
	517 <i>Santolina Chamæcyparissus</i> , L.	C	distinct
	519 <i>Anthemis canescens</i> , Brot. „ <i>montana</i> , L., var. <i>grandiflora</i> „ <i>nobilis</i> , L. „ <i>tinctoria</i> , L.	A C C C	distinct distinct slight distinct
2 Chrysanthem- idinæ.	529 <i>Chrysanthemum atratum</i> , L. „ <i>carinatum</i> , Schousb. „ <i>coccineum</i> , Willd. (= <i>Pyrethrum roseum</i> , Bieb.) „ <i>coronarium</i> , L. „ <i>corymbosum</i> , L. „ <i>ircutiana</i> , Turcz. „ <i>Leucanthemum</i> , L. „ <i>macrophyllum</i> , Waldst. and Kit. „ <i>maximum</i> , Raymond „ <i>præaltum</i> , Vent. „ <i>segetum</i> , L.	O C C C C C C C C C A : B	distinct distinct distinct distinct slight (19) slight but variable slight slow but distinct distinct A distinct, B slight
	530 <i>Matricaria Chamomilla</i> , L. „ <i>inodora</i> , L. „ <i>discoidea</i> , DC.	A : C A : C O	A distinct, C slight A marked, C slight distinct
	533 <i>Cotula coronopifolia</i> , L. 534 <i>Cenia turbinata</i> , Pers. 548 <i>Tanacetum vulgare</i> , L. 551 <i>Artemisia vulgaris</i> , L.	O A : C A (OJ)	A marked, C slight distinct
INULEÆ.			
2 Plucheinæ	173 <i>Pluchea Bulleyana</i> , Jeffrey	C	distinct
4 Gnaphaliinæ	203 <i>Antennaria dioica</i> , Gaert. 208 <i>Anaphalis cinnamomea</i> , C.B.C. „ <i>margaritacea</i> , Benth. 219 <i>Helipterum Manglesii</i> , Muell. „ <i>roseum</i> , Benth. 220 <i>Helichrysum bracteatum</i> , Andr. 225 <i>Cassinia Vauvilliersii</i> , Hk.f. 235 <i>Ammobium alatum</i> , R.Br. 244 <i>Myriocephalus Stuartii</i> , Benth.	(H) C C C A C A C	(20) distinct distinct marked (21) distinct (14) slight distinct slight short, quick movement
5 Angianthinæ	269 <i>Podolepis canescens</i> , A.Cunn.	(OJ)	
7 Athrixiinæ	275 <i>Inula Conyza</i> , DC.	C	slight
8 Inulinæ	„ <i>ensifolia</i> , L. „ <i>glandulosa</i> , Puschk. „ <i>Helenium</i> , L. 289 <i>Pulicaria vulgaris</i> , Gaert. „ <i>dysenterica</i> , Gray.	O C (J) A A : C	distinct distinct distinct distinct A distinct, C variable

TABLE VIII (continued)

Tribe and Sub-tribe.	Genus and Species.	Types of Irritability.	Remarks.
<i>INULEÆ (old.)</i>			
9 Buphthalmineæ	298 <i>Buphthalmum salicifolium</i> , L.	B	distinct
	" <i>speciosum</i> , Schreb.	C	slow
	302 <i>Odontospermum maritimum</i> , Sch.Bip.	C	marked (22)
<i>CYNAREÆ</i>			
1 Echinopsidinae	621 <i>Echinops bannaticus</i> , Rochel.	C	slight
	" <i>cornigerus</i> , DC.	B	distinct
	" <i>dahuricus</i> , Fisch.	C	distinct
	" <i>exaltatus</i> , Schrad.	C	marked
	" <i>Ritro</i> , L.	C	distinct (23)
	" <i>sphærocephalus</i> , L.	C	marked
	" <i>Tourneforti</i> , Ledeb.	C	marked
2 Carlininae	624 <i>Xeranthemum annuum</i> , L.	(J)	
3 Carduinae	631 <i>Arctium majus</i> , Bernh.	C	slight
	633 <i>Carduus cernuus</i> , Steud.	C	marked
	" <i>crispus</i> , L.	C	distinct
	" <i>defloratus</i> , L.	(Kn)	
	" <i>nutans</i> , L.	C	distinct
	" <i>Personata</i> , Jacq.	(Kn)	
	" <i>tenuiflorus</i> , Curt.	B	distinct
	634 <i>Cnicus acaulis</i> , Willd.	C	distinct
	" <i>altissimus</i> , Willd.	(M)	
	" <i>arvensis</i> , Hoffm.	(J)	
	" <i>canus</i> , Roth.	(J)	
	" <i>carlinoides</i> , Fisch.	(H)	
	" <i>Casabonæ</i> , Roth.	(K)	
	" <i>eriophorus</i> , Roth.	B	slight
	" <i>lanceolatus</i> , Willd.	C	distinct
	" <i>palustris</i> , Willd.	C	marked (24)
	" <i>serrulatus</i> , Bieb.	(M)	
	" <i>syriacus</i> , Roth.	(J)	
	634a <i>Cirsium Kernerii</i> X (Hort.)	B	distinct
	635 <i>Onopordon acanthium</i> , L.	(K)	
	" <i>arabicum</i> , L.	(K)	
	636 <i>Cynara Cardunculus</i> , L.	(K)	
	637 <i>Silybum Marianum</i> , Gaert.	C	distinct
	639 <i>Tyrimnus leucographus</i> , Cass.	(J)	
	642 <i>Saussurea albescens</i> , Hk.f.	C	marked
	" <i>Yakla</i> , G.B.C.	C	distinct (25)
4 Centaureinae	648 <i>Serratula coronata</i> , L.	(J)	
	" <i>quinquefolia</i> , Bieb.	C	slight, variable
	653 <i>Leuzea conifera</i> , DC.	C	distinct
	654 <i>Centaurea alba</i> , L.	(M)	
	" <i>americana</i> , Nutt.	(M)	
	" <i>aspera</i> , L.	B	distinct
	" <i>atropurpurea</i> , Waldst. and Kit.	C	slight
	" <i>axillaris</i> , Willd.	C'	distinct
	" <i>calcitrapoides</i> , L.	(Cov.)	
	" <i>cineraria</i> , L.	(K)	
	" <i>concolor</i>	(U)	
	" <i>Cyanus</i> , L.	C'	distinct
	" <i>dealbata</i> , Willd.	C	distinct
	" <i>eriophora</i> , L.	(K)	
	" <i>glastifolia</i> , L.	(K)	
	" <i>Jacea</i> , L.	(J)	
	" <i>macrocephala</i> , Puschk.	(Kb)	

TABLE VIII (continued)

Tribe and Sub-tribe.	Genus and Species.	Types of Irritability.	Remarks.
CYNAREÆ (ctd.) Centaureinæ (continued)	654 <i>Centaurea maculosa</i> , Lam. " <i>montana</i> , L. " " <i>var. alba</i> " " <i>var.</i> <i>lugdunensis</i> , Jord. " <i>Moschata</i> , L. " <i>nervosa</i> , Willd. " <i>nigra</i> , L. " " <i>var. alba</i> " <i>orientalis</i> , L. " <i>præalta</i> , Boiss. & Bal. " <i>pulchella</i> , Ledeb. " <i>pulcherrima</i> , Willd. " <i>ragusina</i> , L. " <i>ruthenica</i> , Lam. " <i>rutifolia</i> , Sibth. " <i>salmantica</i> , L. " <i>Scabiosa</i> , L. " <i>sordida</i> , Willd. " <i>spinosa</i> , L. " <i>variegata</i> , Lam.	(L) C C C (K) (Kn) C C (H) C (Kb) O (K) (Kb) (M) (K) C B (K) C	distinct distinct distinct variable (26) marked distinct (27) distinct marked distinct
	655 <i>Carbenia benedicta</i> , Adans. 656 <i>Carthamus tinctorius</i> , L.	(K & J) C	distinct
MUTISIEÆ. † Gerberinæ	695 <i>Gerbera hybrida</i> , (Hort.) " <i>Jamesoni</i> , Bolus	C ^e C ^e	(28) (28)
‡ Nassauviinæ	702 <i>Perezia multiflora</i> , Less. 708 <i>Moschardia pinnatifida</i> , Ruiz and Pav.	C ^e A: B	(28) A distinct, B variable
VERNONIEÆ. † Vernoniinæ	6 <i>Erlangea tomentosa</i> , S. Moore 16 <i>Vernonia altissima</i> , Nutt. " <i>fasciculata</i> , Michx. 28 <i>Stokesia cyanea</i> , L'Hérit.	O O O O	
ASTEREÆ. † Homochrominæ	79 <i>Grindelia cuneifolia</i> , Nutt. " <i>lanceolata</i> , Nutt. " <i>squarrosa</i> , Dimal. 85 <i>Chrysopsis villosa</i> , DC. " " <i>var. Rutteri</i> 88a <i>Aplopappus croceus</i> , Gray 91 <i>Solidago serotina</i> , Ait. " <i>Virgaurea</i> , L. " <i>piloso</i> , Walt.	O O C C O C C C C	distinct variable distinct distinct very slight distinct
3 Bellidinæ	116 <i>Brachycome iberidifolia</i> , Benth " <i>Thomsoni</i> , Kirk. 117 <i>Bellis perennis</i> , L.	O O C	variable (29)
† Heterochrominæ	119 <i>Amellus annuus</i> , Willd. 121 <i>Chariels heterophylla</i> , Cass. 134 <i>Callistephus hortensis</i> , Cass. 136 <i>Aster acris</i> , L. " <i>alpinus</i> , L. " <i>Amellus</i> , L. " <i>Candollii</i> , Harv. " <i>Curtisii</i> , Torr. & Gray " <i>Lipskyi</i> , (Hort.)	C C C (J) C O O A A: C C ^l	slight distinct distinct slight A distinct, C slight marked

TABLE VIII (continued)

Tribe and Sub-tribe.	Genus and Species.	Types of Irritability.	Remarks.
ASTEREÆ (ctd.)			
4 Heterochrominæ (continued)	136 <i>Aster longifolius</i> , Lam.	C	variable
	„ <i>macrophyllus</i> , L.	(J)	
	„ <i>oreophilus</i> , Franch.	O	
	„ <i>paniculatus</i> , Lam.	A	slight
	„ <i>puniceus</i> , L.	A : B	A distinct, B slight
	„ <i>scaber</i> , Thunb.	O	
	„ <i>sibiricus</i> , L.	O	
	„ <i>stellaris</i> , (Hort.)	C	variable
	„ <i>trinervius</i> , Roxb.	O	
	„ <i>Tripolium</i> , L.	O	
	137 <i>Felicia fragilis</i> , Cass.	C	distinct
	142 <i>Olearia dentata</i> , Moench.	A	very slight
	„ <i>Haastii</i> , Hook.	O	
	147 <i>Celmisia coriacea</i> , Raoul.	C	distinct
	„ <i>petiolata</i> , Hook.	O	
	„ <i>verbascifolia</i> , Hook.	O	(30)
	151 <i>Erigeron aurantiacus</i> , Regel.	A	distinct
	„ <i>Coulteri</i> , Porter	A	distinct (31)
	„ <i>glabellus</i> , Nutt.	A	distinct
	„ <i>grandiflorus</i> , Hook.	A	distinct
	„ <i>macranthus</i> , Nutt.	C	distinct
	„ <i>multiradiatus</i> , Benth. and Hook	C	distinct (32)
	„ <i>Rusbyi</i> , Gray	A : B	A distinct, B slight
	„ <i>speciosus</i> , DC.	A	distinct
5 Conyzinæ	162 <i>Chrysocoma Coma-aurea</i> , L.	C	distinct
EUPATORIÆÆ.			
2 Ageratinæ	54 <i>Ageratum conyzoides</i> , L.	(OJ)	
	66 <i>Eupatorium ageratoides</i> , L.	O	
	„ <i>cannabinum</i> , L.	O	
	„ <i>ianthinum</i> , Hemsl.	O	
	„ <i>perfoliatum</i> , L.	O	
	„ <i>prunellæfolium</i> , H.B. & K.	O	
	„ <i>purpureum</i> , L.	O	
	„ <i>riparium</i> , Regel.	O	
3 Adenostylinæ	73 <i>Liatris callilepis</i> , (Hort.)	O	
	„ <i>spicata</i> , Willd.	O	
HELENIÆÆ.			
2 Baeriinæ	457 <i>Baeria coronaria</i> , Gray	O	
	460 <i>Lasthenia glabrata</i> , Lindl.	O	
	468a <i>Eriophyllum cæspitosum</i> , Dougl.	O	
	476 <i>Palafoxia Hookeriana</i> , Torr. and Gray	(J ?)	
4 Tagetinæ	496 <i>Tagetes erecta</i> , L.	(OJ)	
	„ <i>patula</i> , L.	(OJ)	
	„ <i>signata</i> , Bartl.	(OJ)	
5 Heleniinæ	501 <i>Helenium autumnale</i> , L.	C	distinct
	„ „ var. <i>bicolor</i>	C	distinct
	„ „ var. <i>pumilum</i>	C	slight
	„ <i>Hoopesii</i> , Gray	C	distinct
	502 <i>Gaillardia aristata</i> , Pursh.	(OJ)	(33)
	„ „ var. <i>grandiflora</i>	C	distinct (33)
	„ <i>lanceolata</i> , Michx.	O	

TABLE VIII (continued)

Tribe and Sub-tribe.	Genus and Species.	Types of Irritability.	Remarks.
HELIANTHINÆ			
3 Melampodiinæ	333 <i>Silphium Astericus</i> , L.	O	
	„ <i>integrifolium</i> , Michx.	A	slight
	„ <i>perfoliatum</i> , L.	O	
4 Ambrosiinæ	334 <i>Chrysogonum virginianum</i> , L.	O	
	336 <i>Lindheimera texana</i> , Gray	A	marked
	338 <i>Parthenium integrifolium</i> , L.	O	
	347 <i>Ambrosia artemisiifolia</i> , L.	(OJ)	
6 Zinniinæ	349 <i>Xanthium spinosum</i> , L.	(OJ)	
	„ <i>Strumarium</i> , L.	(OJ)	
	355 <i>Zinnia elegans</i> , Jacq.	C	distinct
	„ <i>Haageana</i> , Regel.	(OJ)	
	356 <i>Sanvitalia procumbens</i> , Lam.	(J)	
	357 <i>Heliopsis lævis</i> , Pers.	C	distinct
7 Verbesininæ	„ <i>padula</i> , Wender.	C	slow but distinct
	„ <i>scabra</i> , Dun.	C	distinct (34)
	„ „ <i>var. gratissima</i> , Lemoin.	C	distinct (35)
	„ „ <i>var. pitcheriana</i>	C	very slow but distinct
	379 <i>Rudbeckia ampla</i> , Nelson	C	distinct
	„ <i>amplexicaulis</i> , Vahl.	(J)	
	„ <i>californica</i> , Gray	O	
	„ <i>hirta</i> , L.	C	see Halsted, 18
	„ <i>nitida</i> , Nutt.	C	distinct
	„ <i>speciosa</i> , Wender.	C	marked
	„ <i>triloba</i> , L.	C	slight
	379a <i>Echinacea angustifolia</i> , DC.	C	see Halsted, 18
	„ <i>purpurea</i> , Moench.	C	distinct
	379b <i>Lepachys pinnatifida</i> , Rafin.	C	see Halsted, 18
	397 <i>Wyethia mollis</i> , Gray	O	
	400 <i>Helianthus annuus</i> , L.	C	slight (36)
	„ <i>debilis</i> , Nutt.	(OJ)	
	„ <i>hirsutus</i> , Rafin.	(M)	
	„ <i>lenticularis</i> , Dougl.	(M)	
	„ <i>micranthus</i> , Spreng.	O	
8 Coreopsidinæ	„ <i>mollis</i> , Lam.	A	distinct
	„ <i>occidentalis</i> , Ridd.	A : C	A distinct, C slight
	„ <i>pumilus</i> , Nutt.	O	
	„ <i>rigidus</i> , Desf.	A : B	A distinct, B slight
	„ <i>tomentosus</i> , Michx.	O	
	405 <i>Helianthella quinquenervis</i> , Gray	O	
	416 <i>Guizotia abyssinica</i> , Cass.	C	distinct
	423 <i>Coreopsis Atkinsoniana</i> , Dougl.	C	slight
	„ <i>Drummondii</i> , Torr. & Gray	(OJ)	
	„ <i>grandiflora</i> , Nutt.	A	slight
	„ <i>Grantii</i> , Oliv.	A : C	A distinct, C slight
	„ <i>tinctoria</i> , Nutt.	A	distinct
	423a <i>Leptosyne Douglasii</i> , DC.	O	
	„ <i>maritima</i> , Gray	A	slight
	„ <i>Stillmannii</i> , Gray	O	
	424 <i>Dahlia coccinea</i> , Cav.	O	
	„ <i>Merckii</i> , Lehm.	O	
	„ <i>variabilis</i> , Desf.	(OJ)	
9 Galinsoginæ	426 <i>Thelesperma filifolium</i> , Gray	O	
	427 <i>Cosmos atrosanguineus</i> , (?)	(J)	
	428 <i>Bidens grandiflora</i> , Balb.	A	slight
	435 <i>Balduinia multiflora</i> , Nutt.	C	slight but distinct
10 Madiinæ	438 <i>Tridax trilobata</i> , Hemsl.	A	slight
	442 <i>Madia dissitiflora</i> , Torr. & Gray	O	
	„ <i>sativa</i> Molin.	O	
	445 <i>Layia gaillardoides</i> , Hook & Arn	C	very slight

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5. In *Senecio clivorum* the filaments are quite unusually thick and rigid.

6. In *Senecio grandifolius* the male stage is very short and the anther tube is frequently split.

7. *Senecio hortensis* seems to be a variety of *S. populifolius*.

8. In *Senecio populifolius* when the anther tube is touched at the proper stage the style protrudes quickly as in *Gaxania*, and the style branches may be seen to diverge immediately the style is exerted and the anthers are retracted sufficiently.

9. The movement is exceptionally difficult to observe in *Senecio vulgaris* as the proper stage is rare on any one plant, and the movement is distinct only during hot weather.

10. The lateral movement in the *Cichorieæ* is slow, and the retraction of the anther tube requires careful observation. It frequently continues after the style branches have diverged.

11. In *Lapsana communis* the straightening of a single filament when touched can be observed easily; the other filaments are seen to become more bent, thus tilting the anther tube in the direction of the stimulated filament.

12. The critical stage in *Taraxacum officinale* is short, and the movement is shown only when the exertion of the style is beginning.

13. *Dimorphotheca Ecklonis* has orange pollen and dark purple stamens, the presentation of the pollen is therefore very easily seen.

14. *Calendula officinalis* and *Helipterum roseum* are recorded by Juel (28) as not irritable, but it must be borne in mind that these show the "A" type only, and that species which are irritable in these latitudes may not show the character further north, cp. *Torenia* (Section B, Chap. III).

15. *Ursinia pulchra* is very variable, showing "A" distinctly under normal conditions in the north (Newcastle), "B" on warm days and "C" under exceptionally favourable circumstances. *U. speciosa* is also very variable, but the "C" type has not yet been observed in this species.

16. For details of the double movement in the stamens and the style in *Arctotis stoechadifolia* and *Gaxania splendens* see Section B, Chap. III).

17. The anther tube in *Achillea macedonica* is frequently split by the style.

18. *Achillea Ptarmica* usually shows "A" distinctly. At 10 a.m. in the north (Forfarshire) it shows "C" slightly, but by noon it shows "C" distinctly.

19. *Chrysanthemum corymbosum* shows no movement until the critical stage when the anther tube is opening, and the style is frequently bent as in *Doronicum*.

20. The irritability in *Antennaria dioica* is described by Hildebrand (23) as similar to that of the *Cynareæ*, so that it probably shows the "C" type.

21. In *Helipterum Manglesii* the movement towards the touch through an angle of about twenty degrees is immediately followed by a movement in the reverse direction of about half that magnitude.

22. In *Odontospermum maritimum* the lateral movement is rapid, and is accompanied by a rapid ejection of the pollen, cp. Mutisieæ, note 28.

23. The movement in *Echinops Ritro* occurs only before the style is exerted, and usually only when the filament itself is touched (see note 24).

24. In *Cnicus palustris* and most other species the lateral movement is greatest when the filament itself is touched, not the anther as has been usual in this investigation.

25. The anther tube in *Saussurea Yakla* projects above the disc just high enough to rub the pollen at the top against the wing of a bee while it is standing on the disc. This mechanism is easily observed while bees are visiting the flower.

26. The variation in the movement in *Centaurea nigra*, sometimes "B" and sometimes "C," is partly explained by the behaviour of the filaments. When the anther tube is touched at one side all the filaments can be seen to become more bent and then to straighten out, at the same time becoming shorter. The two stages seem to give time for one of the filaments other than the nearest one to contract first and the successive contractions give the type "B."

27. This exception (*Centaurea pulcherrima*) in the genus may be explained by the fact that a considerable part of the style is free from hairs and the pollen-presentation begins only after the exertion of the style to a considerable degree.

28. In *Gerbera hybridu* the pollen is extruded in small quantity but more rapidly than is usual in the "C" type: the movement is towards the touch. In *Gerbera Jamesoni* and *Perexia multiflora* the outer florets are much more active than the inner, and the greatest lateral movement is towards the centre of the capitulum. In the former species half the pollen is expelled at the first touch and the rest at the second. In the latter all the pollen

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is expelled at the first touch. This explosive movement has as yet been observed only in the Mutisieæ, and is sometimes so energetic that the pollen is thrown over the edge of the capitulum.

29. The movement in *Bellis perennis* is most active, as in many other species, between noon and 3 p.m., and is sometimes so strong that the anther tube is split against the comparatively thick and rigid style.

30. The anther tube is frequently split in *Celmisia verbascifolia*, cp. notes 2, 6 and 17. This character is also recorded for *Cratistylis conocephala* (49, p. 267, note 8).

31. When repeatedly tested with a cloud over the sun *Erigeron Coulteri* showed no movement, but an hour later with a few minutes of sunshine the "A" type of movement was distinct.

32. The movement is greatest in *Erigeron multiradiatus* when touched so that the reaction is towards the centre of the capitulum.

33. Juel (28) records no irritability in *Gaillardia aristata* and the var. *grandiflora* showed none at 6.30 p.m., but was distinctly sensitive at 10.30 a.m. (Kew).

34. The movement is greatest in *Heliopsis scabra* when it is towards the centre, cp. note 32.

35. In var. *gratissima* of the above species the anthers are forced apart when the filament is stimulated and the pollen is presented along the slit. In the evening the stamens are more or less free from each other, cp. notes 2, 6, 17 and 30.

36. The lateral movement in *Helianthus annuus* is slight and slow, but Gray (13) previously recorded a distinct lateral movement (see Section A, Chap. III). •

The physiology of the movement is discussed in Section D and the phylogenetic significance in Section E, so that it is only necessary to point out some of the chief facts of the distribution of irritability in the family as shown by Table VIII.

Of the three main types, A, B and C, of movement C seems to be the most primitive because it involves only one step—the contraction of one of the five filaments; B involves the transference of the stimulus to the other four filaments, and this occurs in an indefinite order, giving an indefinite lateral movement; A involves the transference of the stimulus to the other four filaments in such an organised fashion that all five contract simultaneously.

In the cases where the A type of movement is recorded as slight it is possible that this is due to an incipient C motion, which would show as such in better conditions. The A type in the Anthemideæ, *Lindheimera*, *Coreopsis* and *Erigeron*, however, seems

to be a distinct movement of a higher type. C' and C^e are obviously special developments of the general C type.

In *Senecio* the C type is the commonest, while allied genera such as *Arnica*, *Cineraria* and *Othonnopsis* show the higher types, A or B. The Tussilagininæ and Vernoniæ with a pollen presentation like that of the Eupatoriæ show no irritability, nor does the latter tribe. The Cichoriæ are distinguished by a peculiar, slow, lateral movement of the primitive C type; this type of movement also occurs in *Senecio Ligularia*, var. *speciosa*. The C type is very active and highly developed in the Calendulæ, notably in *Dimorphotheca*. The Arctotideæ combine an irritable style with the C type of staminal movement. The Anthemideæ and Inuleæ show an increase in the type A movement, while type C remains predominant. Six of the nine sub-tribes in the Inuleæ have been examined and five show irritability. Type B is shown in a number of Cynaræ, and this is to be correlated with the occurrence of the same type in *Buphthalmum salicifolium*. Type C' seems to be confined to the genus *Centaurea*, except for the intermediate stage shown by *Erigeron* and *Heliopsis* (see notes 32 and 34). The explosive type, C^e, is confined to the Mutisiæ.

Five of the six sub-tribes in the Astereæ have been examined and all show irritability, mostly of the C type, but with type A common and developed to a notable extent in *Aster* and even more so in *Erigeron*. Three of the five tribes in the Heleniæ have been examined, and only one (Heleniæ) shows irritability with certainty. This is noteworthy, and is to be correlated with the number of genera in the Heliantheæ which show no irritability. Seven of the ten sub-tribes in the Heliantheæ have been examined, and six show irritability. Irritability is scarcely to be expected in the dioecious forms of the Ambrosiinæ; the predominance of the C type in the Verbesiinæ and the large proportion of the A type in the Melampodiinæ and Coreopsidinæ are to be noted.

D. PHYSIOLOGY OF IRRITABILITY.

Apart from such statements as that of Bose (3) that the stamens in the Compositæ are truly sensitive, Cassini's suggestion (6) of the death of the filaments as the cause, that of Ker (30) that the movement of the style in *Arctotis* is due merely to elasticity and Meehan's similar explanation (41) of the movement of the stamens in *Helianthus*, with the contradictions by Brown (4) and Gray (13-14), considerable progress has been made with the study of the general phenomena of irritability. Smith (51)

discovered the localisation of the irritability in *Berberis* and Goeppert (12) and others followed with physiological studies of that genus. Kabsch (29) seems to have been the first to make a proper physiological investigation of the movement in *Centaurea*. He figures and describes the vascular supply and the tactile hairs. He suggests that the spiral vessels are perhaps responsible for the well-known elasticity of the filaments, and considers that the tactile hairs occur so frequently in all irritable floral organs that they appear to be the chief factor in irritability.

Heckel (22) distinguishes between nutritive irritability with an automatic mechanism as in *Ruta* and functional irritability as in the many other cases where a touch is required to set the mechanism in motion. The latter class can be conveniently sub-divided into those cases where the action is mechanical, as in the explosive stamens of *Urtica*, and those where the response is protoplasmic in origin, as in *Berberis* and the Compositæ.

Pfeffer (45) made the next important contribution, and there is an easily accessible account of this work in his *Physiology of Plants* (46). He shows that in *Berberis* the mechanism is similar to that of the pulvinus in *Mimosa*, and that the structure and distribution of the irritable tissue in *Helianthemum*, etc., cause the stamens to move always in the same direction wherever they are touched. He also shows that the contraction of the filaments in the Cynarææ is due to a loss of turgor, that the filaments contract with a decrease in volume and the exudation of water into the inter-cellular spaces, which are largely developed in the tissue of the filament. The contraction varies from 8% to 30% of the length of the stamens, and as the injection of a .5—1.0% solution of potassium nitrate causes the same amount of contraction Pfeffer concluded that the energy of contraction amounts to from 1 to 3 atmospheres pressure. On these grounds he controverts Cohn (9) and Unger (54-55), who maintained that the filaments broadened as they contracted and that there was no diminution in volume. Cohn also considered that the active contraction of the protoplasm was responsible for the movement, but Pfeffer considered this improbable on account of the high energy of contraction. He also contradicts Hofmeister (24), who suggested that the cell-wall was the responsive part of the cell, although he agrees that the power of contraction lies in the cell-wall, and shows that the filaments after stimulation and contraction when put in boiling water contract 10%—40% of their length more on account of the elasticity of the cell-wall.

Oliver (44) showed that in the case of the stigmas of *Mimulus*

and *Martynia* the transmission of the stimulus was completely independent of the vascular bundle, and that the presence of a well developed system of intercellular spaces confirmed Pfeffer's theory of the extrusion of water and loss of turgor as the cause of the movement. Chauveaud (8) controverts Pfeffer and returns to a position similar to that of Cohn. Minden (42), however, considers that the style of *Arctotis* shows analogies in structure and movement with those described by Pfeffer in the stamens of the *Cynareæ*. The marked effect of the meteorological conditions on the movement of the styles (47) and stamens (49) is another piece of confirmatory evidence. The fact recorded by Harger (21), that if no pollen is placed between the stigmatic lobes of *Martynia* they soon re-open, but with pollen this never occurs, also shows that the movement is no mere mechanical one.

Most of those who have described the tactile hairs, especially Haberlandt (15), consider them to be organs of perception, but Halsted (18) has recorded a movement in at least two species in which no tactile hairs are present. Many of the species given in Table VIII also show no tactile hairs, and Linsbauer (37) regards these hairs when present as stimulators or stimulus-transmitters rather than organs of perception.

It may be considered proved that a loss of turgor when the filament or style is touched is the cause of the movement, and Haberlandt states that "it is not known whether the fall of turgor depends upon a sudden diminution of the osmotic strength of the cell-sap, caused by the external stimulus, or whether the latter brings about an increase of the permeability of the ectoplast towards the osmotically effective constituents of the cell." If we consider that the cell-sap has a much more stable composition than the ectoplast, and that the latter is protoplasmic and therefore in a condition of unstable equilibrium, it is not difficult to see which is the more likely to be affected by a sudden change on being touched. Dr. F. F. Blackman in a recent lecture (London, 1913) suggested that the irritability of the stamens in the *Cynareæ* might be due to permeability changes similar to those in the pulvini of *Mimosa* and *Phaseolus*. The writer (50) has recently shown that the geotropic sensitiveness of the root is due to permeability changes giving a differential loss of turgor and consequent movement. The difference in the time relations of the movement in the root and the filaments is to be explained by the state of tension of the latter and their relative slimmness. In those cases where tactile hairs are absent the same deformation of the sensitive protoplasm may occur in the epidermal cells as probably

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occurs in the tactile hairs when they are touched, thus starting the changes which result in the movement.

It is hoped that the necessary apparatus will be devised presently to prove the similarity, if it exists, in the stimulation of the root and of the stamens, and it may be possible also to test a suggestion that in both cases the first result of the application of the stimulus is a change in the electrical condition of the limiting layer of the protoplasm, which change alters the permeability, and therefore the turgor, giving the elastic cell-walls an opportunity to contract in the case of the filaments and to expand at a relatively greater rate on the upper side in the case of the root.

E. THE PHYLOGENETIC SIGNIFICANCE OF IRRITABILITY

Considering all these facts in the light of the probable lines of evolution (found as a result of the examination of the morphology of the styles and stamens) shown in Fig. 7, Chap. II, the first point to be noticed is that in no case is a sub-tribe which shows irritability derived from one showing no irritability. This fact in itself is very good proof that irritability has followed the same lines of evolution as the morphology of the pollen-presentation mechanism. The second point is that the possible affinities of the Gnaphaliinæ with the Gorteriinæ and Gerberinæ are rendered less probable by the occurrence both in the Gorteriinæ and Arctotidinæ of irritable styles of the same type, and by the occurrence in both the Nassauviinæ and Gerberinæ of an explosive mechanism of a peculiar type. These two pairs of sub-tribes seem to be more intimately connected than is suggested by the morphology of their styles and stamens. The development of the A type in several distantly related groups is not of great importance, as that type of movement is a logical development in the evolution of irritability.

The Cichorieæ are again isolated on account of the peculiar, slow movement of the anther tube, which movement, however, is also shown by *Senecio Ligularia*, var. *speciosa*.

The Tussilagininæ, Vernoniæ, Eupatoriæ, Ambrosiinæ and Athrixiinæ are all end groups derived from groups in which irritability is present, so that the absence (as yet) of records of irritability for these groups does not in any way invalidate the previous arguments. As before the Othonninæ cannot be distinguished from the Senecioninæ, nor can the various tribes of the Cichorieæ be separated from each other with any certainty.

The Calenduleæ show a marked development of the C type in *Dimorphotheca*, thus confirming the affinity with the Senecioninæ.

The Arctotideæ are again isolated on account of their irritable

styles, but by the same phenomenon the tribe is shown to be more homogeneous. The occurrence of types A and B, as well as C, but no irritable style in *Ursinia* is very interesting as that genus was suggested (Chap. II, E) as the primitive genus in the tribe.

The two sub-tribes in the Anthemideæ again cannot be distinguished.

The large development of irritability (90% or 18 out of 20 species) in the Inuleæ is quite in accordance with the suggested derivation of the Cynareæ from that tribe, and the marked movement in *Odontospermum* and the occurrence of the B type in *Buphthalmum* also support the same suggestion. Only one of the Cynareæ examined (*Centaurea pulcherrima*) showed no irritability, but the pollen-presentation is somewhat anomalous, and further investigation is required. Irritability is highly developed in this tribe, and the type A movement is combined in a marked degree with the lateral movement of the C type, so that the advanced position of the Cynareæ is maintained.

In the Mutisieæ it was suggested that the Nassauviinæ was the primitive group, and this is supported by the occurrence of the A and B types in *Moscharia* of that sub-tribe and the development of the explosive mechanism in *Perezia* and the Gerberinæ.

In the Astereæ the absence of the A type from the Homochrominæ and the Conyzinæ may be taken as the forerunner of the complete absence (by disappearance) of irritability in the Eupatorieæ, or it may be that the Heterochrominæ with type A is the higher group. The development of the A type in the Heterochrominæ confirms that group as one in advance of the Senecioninæ, while the absence of the A type in the Bellidinæ is to be explained by its relative nearness to the primitive stock.

The Heleniæ are particularly interesting. On account of their comparatively advanced stamens (types 4-6) the Heleniinæ were placed above the Tagetinæ (type 3), but were derived from the stock before the latter on account of the simplicity of their styles (type IV) as compared with the Tagetinæ (types VII-VIII). Now, while the latter shows no irritability, the Heleniinæ do so to a large extent. The other sub-tribes were derived from the Tagetinæ, and show no irritability.

In the Heliantheæ the A type movement, which is undoubtedly distinct from the C type, occurs in the Coreopsidinæ and Melampodiinæ, two sub-tribes which are placed in the same line of evolution in the original phyletic scheme.

We, therefore, come to the conclusion that the evolution of the sub-tribes suggested in Fig. 7, Chap. II, is confirmed by the

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study of the irritability of the pollen-presentation mechanism in every point upon which we can bring it to bear in the present strictly limited condition of our knowledge of the distribution of irritability in the family. There are many gaps which it is hoped to fill by a more extensive study of the phenomenon.

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CHAPTER IV.

THE COROLLA.

THE main characters of the corolla may be divided into four groups—form, development, colour and vascular anatomy, and, in addition to the presentation of the facts concerning these characters, the present chapter includes the history of our knowledge of the corolla in the Compositæ and a discussion of the bearing of the facts and the theories of variation in the corolla upon our general problem of the origin and development of the family.

A. HISTORY.

The history of the corolla begins with the observation by Theophrastus (see Chap. I, Section A) of its epigynous position. During the period of the herbals very little attention was paid to the floral characters. Among the early writers, Lobel (49) seems to have considered the corolla in grouping his genera and Caesalpino (14) used the colour of the corolla to sub-divide his Class XI, the Anthemides, which included practically all the Compositæ not in the Cynareæ or Cichorieæ.

Morison (57) used the colour of the corolla and the presence or absence of rays in his sub-divisions of the Compositæ; Ray (69) and many systematists in the succeeding period followed his example. The discoid, rayed and “semi-flosculose” (Cichoriaceous) condition of the corolla furnish the diagnostic characters for the main divisions of the family in Tournefort’s system (81). Boerhaave (8) separated the Cynareæ from the other discoid forms and endeavoured to place these latter among related genera, distinguishing radiate and discoid forms.

After the definite establishment by Vaillantus (86) of the sections, Cynarocephalæ, Corymbiferæ and Cichoraceæ very little advance was made in the use of the characters of the corolla until Cassini published his analysis of the corolla (16); the chief point to be noted is the establishment of the Labiatifloræ (Mutisieæ) by De Candolle and Lagasca. Berkhey, in 1760, (7) considered the corolla in some detail but added nothing new. Gaertner, in 1791

(31), returned to the Radiatæ and Discoideæ of the earlier systematists. Bentham (see Bib. I, 7) confirmed Brown's statement (10) of the universality of the valvate aestivation of the corolla in the family and considered the characters of the corolla as important for purposes of classification. Robertson (72) mentions a curious point concerning the receptacular bristles in *Echinacea* spp., which protect the flowers from bees and adapt them to butterflies by increasing the functional length of the nectar tube beyond that of the corolla.

The only observations of the "absciss-mechanism" of the corolla seem to be those by Yapp (98).

In connection with the popular explanation of the enlargement of the corolla of the ray florets at the expense of the stamens, Uexküll-Gyllenband (85) adduces numerous examples of (1) reduction in the stamens with no reduction in the corolla, (2) enlargement of the corolla with no reduction in the stamens, (3) reduction in the stamens with reduction also in the corolla, and (4) reduction in the stamens with both enlargement and reduction of the corolla in the same species. It may, therefore, be considered proved that there is no correlation between the enlargement of the corolla and the absence of the stamens in the ray florets.

The detailed history of the corolla subsequent to Cassini may be most conveniently given in various sections as follows:—

Development. The first account of the floral development in the family is by Buchenau (12, 1854), who extended his observations in a later contribution (13). Two years later Cruger (22) showed clearly that the corolla was differentiated before the pappus, and the following year the study of the subject reached its highest point in Payer's clear and elaborate exposition (67). Payer confirmed the late appearance of the "calyx" and the early appearance of the posterior split in the Cichoriæ. Weber (89) considered that the corolla in the Cichoriæ and that of the ray florets in other tribes is an entire tube which is split only by the growth of the style and stamens when the corolla is quite mature. Kohne (46), Buchenau (13) and Payer (67) all agree in observing the early posterior split in the Cichoriæ and the abortion of the posterior lip in the ray florets. Hildebrand (36) gives the usual account with a few figures, but Payer's figures are the best yet published. Cramer (21) treats of the Compositæ, but considered only the ovule in detail.

Our knowledge of the development of the corolla was extended to the "Labiatifloræ" by Hänlein (35) who considered that the

bilabiate corolla showed a development intermediate between that of the ordinary ray corolla and that of the tubular corolla.

Coulter (20) considered that the primordia of all four sets of floral organs are blended at first and that the late appearance of the calyx is due only to the late development of its upper portion. Martin (51) agrees with Coulter and points out that of necessity the "calyx-tube" must be the first part to appear. As no demarcation can be observed between the ovary wall and the so-called calyx-tube it would seem more in accordance with modern nomenclature to describe the undifferentiated primordium as the receptacle of the flower.

The most recent contributions are those by Merrell on *Silphium* (54) and by the writer on *Senecio*, *Calendula* and *Taraxacum* (81). Merrell again confirms the corolla as the first floral part to be differentiated and goes into many interesting details of the other parts of the floret.

Colour. Hildebrand in his elaborate treatise (37) includes a number of observations on the Compositæ. He established the colour sequence—green, yellow, white, red, violet, blue—by observing the following facts—blue flowers vary to violet, red and white but seldom to yellow; red flowers vary more to yellow than do blue flowers; yellows may vary to blue but more often to red; green flowers give yellow and white flowers; yellow gives orange with red plastids and the colour of the sap gives reds and blues.

Müller's contributions are extensive but he gives two very useful historical accounts (60-61). The views expressed in one of

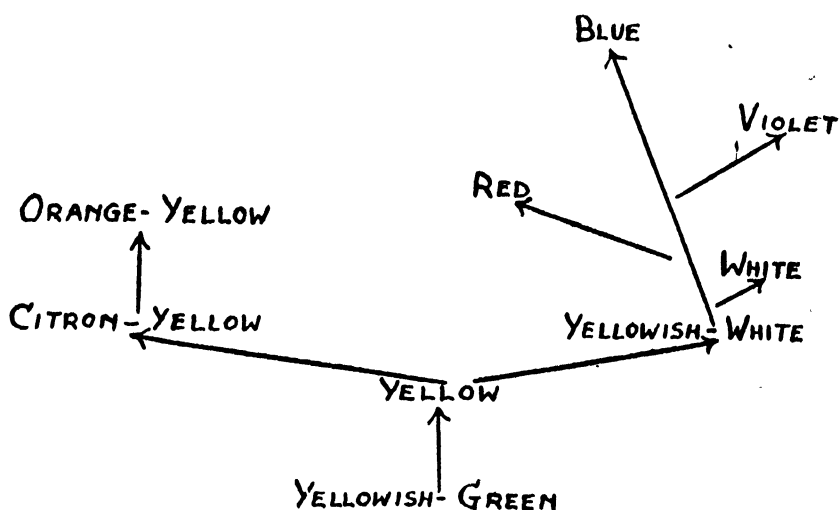


FIG. 8. Evolution of colour according to Müller.

his earlier papers (58) may be given as a diagram, Fig. 8. In his *Alpenblumen* (59), Table II, p. 481, his figures for the insect visitors to yellow and to white flowers are very similar, but he gives the colour sequence—greenish-yellow, yellow, yellow with orange red spots, white, white with yellow spots, rose red, deep red. From other tables butterflies, and even bees, seem to prefer yellow to white.

Avebury (2) considers that blue flowers have evolved from green flowers by passing through the intermediate stages of white or yellow and generally red.

Grant Allen (1) gives a similar colour sequence, but in considering the *Compositæ* he takes the *Cynarææ* as primitive on account of their highly developed colours and states that reversion in colour has been the rule throughout the family because "the primitive ancestral composite had reached the stage of blue or purple flowers while it was still at a level of development corresponding to that of the scabious or *Jasione*." He also considered that the "Ligulates were again developed from the yellow-rayed *Corymbifers* by the conversion of all the disk florets into rays."

Observations by Willis and Burkill (92) confirm the general sequence. Table XII (92a) shows yellow above white but Table XIII (*loc. cit.*) shows a decided preference by the higher insects for white.¹ In most of the tables given white is seen to be preferred to yellow by desirable visitors and in Table XXXVII (92b) the order of efficiency is given as—rose purple, blue, lilac, white, yellow, green.

De Vries (87-88) gives many examples in the *Compositæ* of the atavistic variations noted by Hildebrand (37) and also progressive variations where white flowered species have suddenly developed blue varieties, such as *Ageratum cœruleum*. A similar progressive mutation, where a white ray appeared in one capitulum of a normally yellow flowered *Dahlia*, is discussed in its biochemical aspect by Kajanus (45). Other sudden variations in colour are recorded in *Cosmos* by Longo (50). An interesting atavism is recorded by Daniel (23), see also Small (77).

Anatomy. Jacquin (43) and other early botanists who figured the corolla in the *Compositæ* did not usually indicate the venation accurately; usually a vein is put in the position of the midrib for

¹ There are several kinds of whites, see Neilson Jones (64a).

each lobe (see Jacquin, plates 589-595). Berkhey (7) is an exception as he shows the veins correctly in his figures.

Brown (10) was the first to observe the venation of the corolla in detail and gives the disposition of the veins (alternating with the corolla lobes and dividing, then uniting to form an arch to each lobe) as a remarkable point common to all Compositæ. On this character he controverted the removal of the Ambrosiinae from the Compositæ as carried out by various authors from Linné downwards (see Table I, Chap. I). In a later contribution Brown (9) gives an account of the history of this subject up to his date, 1818.

Don (27) at a later date duly noted the venation of the Cichoriaceous corolla. He also discussed the vascular supply in *Zinnia* (28) and considered that the corolla was absent in that genus, on account of the peculiar veining of the structure; the ray being "an elongation of the exterior cortical layers of the ovary."

Hildebrand (36) gives very good details in Plate I, Fig. 6, of the vascular supply of the corolla in *Taraxacum* and also in other types. The only detailed observations of the vascular supply of the corolla are those by Trécul (83, see also 76) and those by the writer (76).

Anomalous Structure. Anomalies in the structure of the flower, especially the corolla, are dealt with in detail by Masters (52) and at greater length by Worsdell (97). It is, therefore, necessary to point out only a few marked or additional facts.

There are a number of records of floral anomalies in *Helenium autumnale*. The most complete account is that by Worsdell (96). Other accounts have been given by Masters (53) and the writer (77). A proliferation similar to that which occurs in *Helenium* is recorded by Békétoff (6) for *Cichorium Intybus*.

The proliferation known as the "hen and chickens" occurs frequently in a number of genera, see Worsdell (97) and Offner (65). Daniel (24) records some interesting grafting experiments where the interaction of the scion and stock extended to the number of capitula developed.

Depauperation occurs frequently. James (44) gives an account of a solitary capitulum instead of numerous capitula in *Rudbeckia hirta*, but genera with branched inflorescences frequently have one or more more species in this condition, a notable example being *Liabum*, § *Paranephelium*, and a more remarkable example outside the family, *Gardenia Thunbergia*, Rubiaceæ (79).

Another form of depauperation is a reduction in the number

of florets in the capitulum. *Madia sativa* usually has about 25 disc florets and 10 ray florets. *Madia dissitiflora* usually has 3-6 disc florets and 5-8 ray florets. Specimens of these two species were grown in pots in 1916 at Newcastle and both showed only two or three disc florets and two to four ray florets. A similar phenomenon is recorded in *Anthemis Cotula* (3), where the disc florets were entirely absent and from 6-20 ray florets, arranged in the "double" fashion, remained. Fasciated capitula are common, see Worsdell (97), Bailey (4), Bruckman (11) and Palibine (66a).

Two very curious anomalies are the common, if not constant, occurrence of loose florets on the root stocks of *Catananche lutea*, which is recorded by Daydon Jackson (42), and the so-called supernumerary petals recorded by De Candolle (15).

Anomalous Bilabiate Florets. One of the earliest indications of this anomaly is the description of the four-toothed corolla of *Erigeron humile* by Graham (34). Eichler figures (30, p. 286) a bilabiate corolla in *Xeranthemum annuum*. Giard (33, Plate I, Fig. 2) figures a few bilabiate, neuter, ray florets in *Pulicaria dysenterica*. Celakowsky (17, and see Worsdell, 97, Plate 39) figures a similar structure in *Anthemis austriaca*. Uexküll-Gyllenband (85) figures a two-lipped corolla in *Psiadia glutinosa*, *Heterothalamus brunioides*, *Xeranthemum annuum*, *Erigeron alpinus*, *Centaurea Jacea*, (see Fig. 4, Chap. II), also in *Denekia capensis* and *Petasites* spp. Wettstein (91, p. 468) figures the same phenomenon in *Plagiocheilus peduncularis*. Trow (84, p. 274) figures an irregularly bilabiate corolla in *Senecio vulgaris*. Hoffman (38), in addition to several of the above, figures a bilabiate corolla in *Grangea maderaspatana*. Other examples are *Helenium autumnale* (Fig. 9, 9) and *Chrysanthemum Leucanthemum* (see Traverso, 82). The writer has figured bilabiate forms in *Calendula* and *Dimorphotheca* (77, see Fig. 9, 10-11). The reduced corolla of the honey flowers in *Leontopodium alpinum* recorded by Uexküll-Gyllenband (Fig. 4, Chap. II) were first mentioned by Schröter (73). Müller (61a) and Boeuf (7a) record cases of polymorphism with changes in the size of the corollas of the outer florets.

Chrysanthemum Leucanthemum, var. *tubulifera*. Dickson (26) exhibited specimens of this anomaly, where the ray florets are tubular as is frequently the case in *Helenium autumnale*, at the British Association, in 1874. Stevens (80) in 1907, and Traverso (82) in 1911 figured various other irregularities, in the rays of this species.

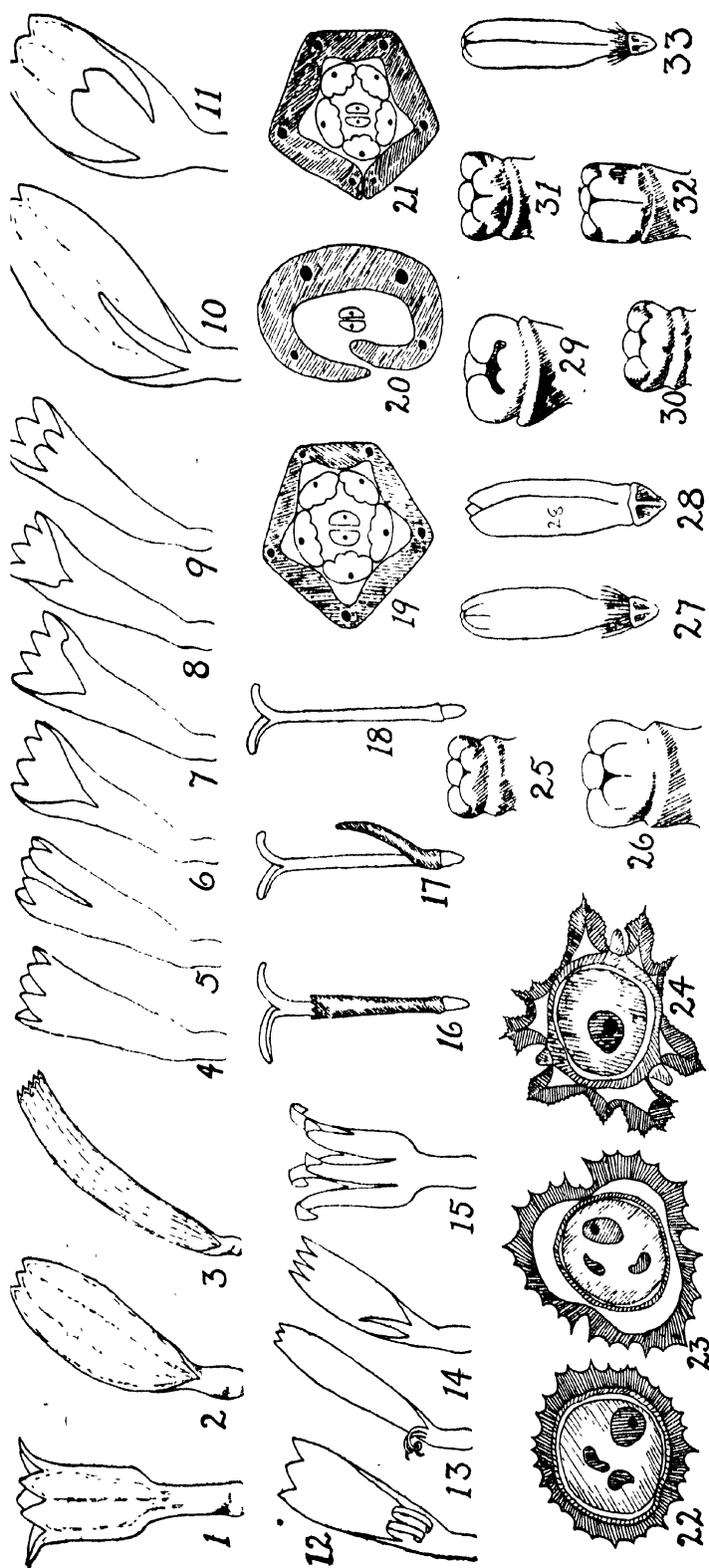


FIG. 9. 1-3, typical corolla forms. 4-9, corolla forms in *Helianthemum autumnale*. 10, corolla in *Calendula officinalis*. 11, corolla in *Dimorphotheca pluvisalis*. 12-15, corolla forms in the Mutisieae. 12—*Irixia*, 13—*Trichotome*, 14—*Barnadesia*, 15—*Schlechtendahlia*. 16-18, female florets in *Haastia Sinclairi* (after Uexküll-Gyllenband); the corolla is shaded. 19-21, transverse sections of young florets, oriented with axis to left of figure. 19—tubular, 20—bilabiate, 21—ligulate. 22-24, sections of types of pollen grains. 22—*Tubuliflorae*, 23—*Senecio vulgaris* (occasional form), 24—*Cichorieae* (after Beer). 25-33, floral development. 25-27, tubular florets of *Senecio vulgaris* 28-30, ray florets of *Calendula officinalis*, 31-33, ligulate florets of *Taraxacum officinale*.

Recently the phenomenon was again recorded for Britain by Rea (70) and was named as above in an account by Lindfors (48).

The occurrence of similar tubular ray florets in *Helianthus annuus*, *Ratibida columnifera*, var. *tubularis*, *Rudbeckia hirta*, var. *tubuliforme*, and *Gaillardia pulchella*, var. *fistulosa* (*G. fistulosa*, Hort.) is recorded by Cockerell (19), and in *Gaillardia aristata* by Robbins (71).

Mutations. The sudden appearance of these various anomalies adds strength to the evidence for discontinuous variation in the Compositæ. Many examples of such mutations in the corolla and other parts are given by De Vries (87), the origin of *Chrysanthemum segetum-plenum* (88) being a particularly clear case of the origin of a variety suddenly under experimental conditions. The origin in nature by mutation of *Arctium minus laciniatum* is discussed by Hus (40).

Ostenfeld (66) has studied the origin of micro-species in *Hieracium* under experimental conditions and gives as his opinion that "very probably, in Europe, new forms of this sub-genus (*Archihieracium*) are appearing at the present time, and it is an interesting fact that many of the described species have an extremely limited distribution, which points to a very recent origin." This last phrase is of great interest in connection with Willis's Law of Age and Area (94 and 74a) which will be discussed later.

Trow (84) has also recorded a mutation in *Senecio vulgaris* and Ishikawa's cytological work (41) seems to indicate the presence in the Compositæ of tetraploid mutations and "pairs of species" as described by Gates (32). Phillipi (68) records another mutation in *Senecio vulgaris*, a gynodioecious strain.

The anomalous genus, *Fitchia*, was placed in the Cichoriæ by Hooker (39); Nadeaud suggested at first (63) that it should be in the Helianthæ but afterwards (64) agreed with Hooker. Del Castillo (29) subsequently placed the genus in the Mutisiæ. Such cases are best regarded as large mutations like those claimed by Willis (93) in the Podostemaceæ, and their study in the light of modern evolutionary ideas, such as suggested by Davenport (25), is sure to be a great help in the attainment of the truly natural classification, which is the aim of the present and future investigations.

Doubling. In addition to the numerous cases of doubling discussed by De Vries (87-88), Molliard describes some interesting

observations on the causes of doubling in various capitulate species (55-56a). In the Compositæ he mentions a doubling of *Matricaria inodora* as due to *Peronospora Ratii* (56), and in *Bellis perennis* as due to *Eriophyces* sp. (56a).

More or less closely allied to the phenomenon of doubling is the number of ray florets but as this and the number of involucre bracts and receptacular paleæ seem to be expressions of the relation of phyllotaxis to mechanical laws (see Church, 18, Fig. 46, etc.) the whole matter will be discussed latter in a chapter on phyllotaxis.

B. VARIATION IN FORM OF THE COROLLA.

The main thesis of this section is that the ordinary ray floret of the tribes other than the Cichoriæ has really a bilabiate structure, the inner lip being aborted as a rule but frequently more or less developed. It is, therefore, considered advisable to restrict the use of the term *ligulate* to the five-toothed, properly strap-shaped corolla of the Cichoriæ. The fundamental type, as is well shown by Uexküll-Gyllenband (Fig. 4, Chap. II), is the tubular corolla with a campanulate upper region and five equal lobes. In addition to these three types there is a very narrow, tubular form, Fig. 10, A, which is described as filiform.

The Ligulate Type.

As will be shown later (Section C) the ligulate corolla is easily derived directly from the tubular type by a simple splitting or rather by the failure of the connecting tissue to develop between the two posterior petals. The extreme uniformity of this character in the Cichoriæ confirms the conclusion from the uniformity of the pollen-presentation mechanism that the Cichoriæ are monophyletic. The origin has been suggested to be mutational by the writer (77), who also suggested a recent derivation from the Senecioneæ and gave as confirmatory evidence of the Senecioneal origin the occurrence of a type of pollen grain in *Senecio* (Fig. 9, 23) which is intermediate between the characteristic type of the Tubulifloræ, (Fig. 9, 22), and that of the Cichoriæ as figured by Beer (Fig. 9, 24).

The origin of the Cichoriæ by mutation involves only two marked changes, the development of the ligulate corolla and of laticiferous vessels. The problem presented by the latter change is being investigated and as a first step the latex has been shown to be translocated after the manner of carbohydrates (74). The occurrence of transitions from the ordinary mucilage sacs to laticiferous vessels and the development of laticiferous tissue of

various forms in comparatively distantly related genera favours the assumption that this change can take place with comparative ease.

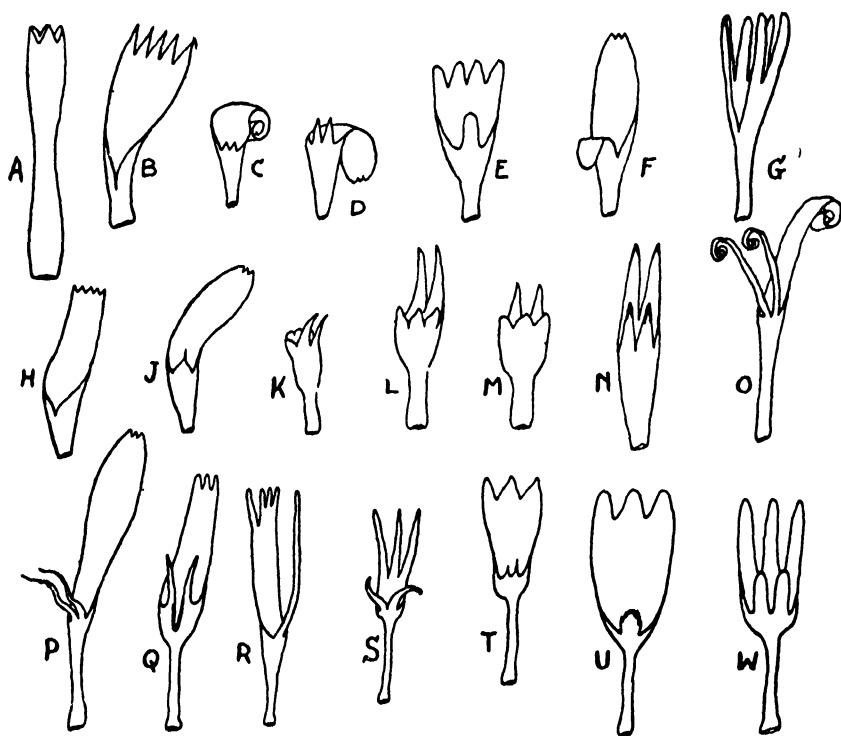


FIG. 10. Corolla forms—A, *Cavea tanguensis*, filiform; B, *Stokesia cyanea*; C, *Brachyglottis repanda*, ray; D, *Nassauvia axillare*; E, *Nanothamnus sericeus*, disc; F, *Dipterocome pusilla*, ray; G, *Ainsliaea pteropoda*; H, *Catamixis baccharoides* (after Thomson); J, *Cryptostemma calendulacea*, ray; K, *Anacyclus clavatus*, disc; L, *A. clavatus*, var. *inconstans*, disc; M, *A. tomentosus*, disc; N, *Siebertia pungens*; O, *Mutisia lanata*, disc; P, *M. lanata*, ray; Q, *Erythrocephalum zambesiaceum*, ray; R, *Seris polymorpha*, ray; S, *Hinterhubera columbica*, one variation of ray; T, *Tridax Mandonia*, ray; U, *Monolopia major*, ray; W, *Microspermum debile*, ray.

The origin of the ligulate corolla can scarcely be other than a discontinuous variation, as there is no genus in the Tubulifloræ which shows even rarely the true ligulate corolla. The five-lobed, palmate corolla of *Stokesia* (Fig. 10, B) and the sub-palmate, five-lobed or five-toothed corolla, which occurs rarely in some species of *Elephantopus* (Veroniceæ), *Pentachæte*, *Lessingia*, *Pterigeron* (Asteræ), *Chromolepis* (Heliantheæ), *Cephalophora*, *Helenium* (Heleniæ), *Chrysanthemum* (Anthemideæ), *Senecio* (Senecioneæ) and more commonly in several genera of the Cynareæ and Mutisieæ, are ob-ovate and palmately lobed, not oblong with practically parallel margins and five triangular teeth like the corolla of the Cichoriæ.

This palmately lobed corolla is only one particular case of the

very varied development of the bilabiate type. The series given, Fig. 9, 4-9, for *Helenium autumnale* includes one, Fig. 9, 5, which belongs to the palmate type and two others, Fig. 9, 7-8, where the abortion of the fifth lobe is progressing to the complete absence shown in Fig. 9, 6.

The origin of the ligulate type by a mutation seems very similar to the origin of the fimbriate type described by Trow (84). The dropping out of a factor for non-ligulateness in the same way as the supposed factor for non-fimbriateness is suggested to have done, would, with the addition of the presence of laticiferous vessels, give the first of the Cichorieæ.

The Bilabiate Type.

The presence of the posterior lip of the bilabiate corolla occurs markedly in the Mutisieæ, where it is characteristic of four of the sub-tribes and occurs in *Seris* (Fig. 10, R) and *Ainsliaea* (Fig. 10, G) of the Gochnatiinæ, but it is by no means confined to that tribe. In addition to the sporadic appearance of the posterior lip described in *Xeranthemum*, *Pulicaria*, *Anthemis*, *Psiadia*, *Heterothalamus*, *Erigeron*, *Centaurea*, *Denekia*, *Petasites*, *Plagiocheilus*, *Senecio*, *Helenium*, *Chrysanthemum*, *Calendula*, *Dimorphotheca* and *Grangea* the phenomenon has been observed by the writer to occur occasionally in the double varieties of *Callistephus*, *Chrysanthemum*, *Helianthus*, and *Tagetes*.

One of the posterior petals is frequently developed in the ray florets in most of the tribes giving a 4-dentate or 4-lobed corolla. The usual number of lobes in the anterior lip is three, but these may be fused to give two or the lip may be entire.

In the Senecioneæ a posterior lip is sometimes developed in the filiform florets of *Erechtites* and it is a normal character of the uniseriate rays in *Brachyglottis*, a monotypic genus very closely allied to *Senecio*, Fig. 10, C.

The posterior lip is also developed frequently in the rays of the monotypic genus, *Dipterocome*, in the Calenduleæ (Fig. 10, F).

In the Arctotideæ *Cryptostemma* shows the character (Fig. 10, J).

In the Anthemideæ *Anacyclus*, § *Diorthodon*, D.C. has the ray entire or 3-dentate but the disc florets although sometimes regularly 5 lobed, are frequently bilabiate, the two posterior lobes being narrow and erect while the anterior lip has the normal form (Fig. 10, K-M).

In the Inuleæ *Nanothamnus*, another monotypic genus, has one of the posterior petals of the hermaphrodite florets split off from the

other four down to the base of the limb, thus giving a bilabiate corolla (Fig. 10, E). Throughout the tribe there are many filiform corollas with the apex bi-dentate or bi-fid; this is another modification of the bilabiate corolla.

The outer florets in the Cynareæ show various bilabiate forms, as in *Centaurea* (see Fig. 4, Chap. II). In *Xeranthemum* (Fig. 4) and *Siebera* (Fig. 10, N) the corolla of the female florets is constantly bilabiate with the anterior lip entire or 2-dentate and the posterior lip divided in two.

The predominance of the bilabiate corollas in the Mutisieæ has already been noticed. In *Barnadesia* (Fig. 9, 14) all or only the exterior florets show a 4 + 1 type of bilabiate corolla. In the Onoseridinæ the bilabiate corolla as a rule occurs only in the 1-3-seriate ray florets, but in *Mutisia*, the largest genus, the condition sometimes extends to the disc florets also (Fig. 10, O-P). The anterior lip has 2-3 lobes or is entire (*Erythrocephalum*) and the posterior lip has two lobes (Fig. 10, Q). The capitulum in the Gochnatiinæ is homogeneous as a rule, but in *Seris* and *Ainslia* an inequality in the length of the laciniae of the corolla makes it sub-bilabiate. The Gerberinæ show great variety in the structure of the two lips. All the florets in the capitulum are usually bilabiate, the anterior being entire or 1-4-lobed and the posterior lip entire, two-lobed or absent. The entire posterior lip is due to the fusion of the two lobes or more frequently to the development of one of the posterior petals with the anterior lip to give a 4 + 1 combination, Fig. 9, 14-15, instead of the usual 3 + 2, Fig. 9, 12-13. The complete abortion of the posterior lip makes the ray floret an ordinary one. In the monotypic genus, *Catamixis*, all five petals are fused and the split is posterior so that something like a ligulate corolla results (Fig. 10, H), but this is just one more variation in the manner of splitting and cannot be taken as an intermediate type leading to the Cichorieæ. In the Nassauviinæ all the florets in the capitulum are bilabiate, usually with the 3 + 2 combination (Fig. 10, D), but the anterior lip is entire in *Oxyphyllum* and various other genera show combinations and fusions of the lobes such as 4 + 1, 3 + 1, 2 + 1, 2 + 2 and 1 + 1.

All these variations prove that the corolla in the Mutisieæ is in a very mutable condition and, in spite of the explosive irritability discussed in Chap. III, it is possible that the Mutisieæ is not a natural group but a collection of bilabiate forms with the addition of the genera of the Gochnatiinæ, which are scarcely to be

distinguished from the Cynareæ. That a bilabiate corolla is not a character of tribal rank is obvious from the large number of cases where it occurs in other tribes.

In the Astereæ the corolla of the ray florets in *Hinterhubera* (Fig. 10, S), *Remya* and *Nidorella* is bilabiate.

The only genus in the Heliantheæ which shows normally a bilabiate corolla is *Tridax*. Here the corolla of the ray floret is of the 3 + 2 type in some species (Fig. 19, T), the two posterior lobes being distinct in *T. decumbens*, L. and very small or completely aborted in the other species, such as *T. angustifolia*. The position of this genus in the Galinsoginæ strengthens the affinity suggested (Fig. 7, Chap. II) between that sub-tribe and the Helenieæ, where the bilabiate corolla occurs occasionally in several genera.

These genera of the Helenieæ are—1, *Monolopia*, where the posterior lip takes the form of a small protuberance (Fig. 10, U). 2, *Chænactis*, where forms like those given for *Helenium* occur (see Fig. 9, 4-9). 3, *Bahia*, where the corolla is sometimes unequally and obliquely divided into four or five lobes. 4, *Microspermum*, where the outer florets have normally the 3 + 2 type of bilabiate corolla (Fig. 10, W). 5, *Pectis*, where the disc florets have the corolla sometimes unequally 5-lobed. 6, *Helenium*, (see Fig. 9, 4-9).

In all cases where there are only one or two rows of ray florets they are apt to disappear giving discoid capitula. This occurs in all tribes but especially in the Senecioneæ and Anthemideæ, see list given by Murr (62).

The Filiform Type.

The term filiform is applied to the very narrow tubular corolla (Fig. 10, A) without the expansion into a limb at the top, as in the ordinary campanulate, tubular corolla. It is more or less characteristic of the Inuleæ, which Bentham divides into two series, the first five sub-tribes with the female florets filiform, and the other four with the female florets bilabiate. This plasticity of the corolla in the outer florets in the Inuleæ is to be compared with the similar plasticity in the Cynareæ.

Outside the Inuleæ this type of corolla occurs only in *Aphantochæte*, *Olearia*, *Erigeron*, *Conyza*, *Haastia*, *Psiada*, *Adelostigma* and *Baccharidina* in the Astereæ and *Homogyne* in the Senecioneæ. In *Erigeron* the female florets are usually bilabiate and very narrow or capillary, but the female florets towards the interior of the capitulum are sometimes filiform.

This fliform type is clearly another modification of the basal type, the tubular campanulate corolla. It is frequently only 2- or 3-lobed at the apex and is, therefore, considered to be derived from the basal type through the bilabiate type by an elongation of the tube and reduction in the lips. This accounts for its femaleness and its position near the margin of the capitulum and also for the transitional stages where the outer florets are bilabiate and some of the inner florets fliform.

Analysis of the Corolla Forms.

The occurrence of these various types throughout the family may be briefly summarised thus :—

Senecioneæ—Tubular, bilabiate with the posterior lip developed sometimes, fliform in *Homogyne* and palmate in anomalous cases.

Cichorieæ—Ligulate.

Calenduleæ—Tubular and bilabiate with the posterior lip developed sometimes.

Arctotideæ—ditto.

Anthemideæ—ditto, and sub-palmate in anomalous cases.

Inuleæ—Tubular, bilabiate with the posterior lip developed sometimes, and fliform in the *Tarchonanthinæ*, *Plucheinæ*, *Pilagininæ*, *Gnaphaliinæ* and *Angianthinæ*.

Cynareæ—Tubular, bilabiate with the posterior lip developed sometimes, and sub-palmate in a number of genera.

Mutisieæ—Tubular, bilabiate with the posterior lip developed frequently, and sub-palmate in a number of genera.

Vernonieæ—Tubular, palmate in *Stokesia* and sub-palmate in *Elephantopus*.

Astereæ—Tubular, bilabiate with the posterior lip developed sometimes, fliform in the *Conyzinæ*, *Baccharidinæ* and a few other genera, and sub-palmate in several others.

Eupatorieæ—Tubular.

Heliantheæ—Tubular, bilabiate with the posterior lip developed sometimes, and sub-palmate in *Chromolepis*.

Helenieæ—Tubular, bilabiate with the posterior lip developed sometimes, especially in the *Heleniinæ*, and sub-palmate in several genera.

Reduction in the Corolla.

The idea that the fliform corolla is derived from the bilabiate

type receives confirmation in the tendency to complete abortion of the corolla in the female florets of several of the genera showing the filiform type, namely *Erigeron*, *Conyza*, *Haastia* (Fig. 9, 16-18), *Psiadia*, *Baccharis* (Astereæ), and *Gnaphalium* (Inuleæ). This tendency is also shown by *Heterothalamus* in the Astereæ, *Clibadium* and *Iva* in the Heliantheæ, *Doronicum* and *Petasites* in the Senecioneæ, and *Leria* in the Mutisieæ. Apart from their bearing on the origin of the filiform corolla, these cases serve to emphasise the tendency to reduction of the corolla material which is general in the family.

This tendency towards reduction is one of the *critical tendencies* which Wernham (90) regards as "no less important than critical characters." In considering the Campanulatæ, however, Wernham noted the tendency to aggregation of the florets and apparently concluded that reduction followed in the relation of effect to the cause (aggregation). It has been pointed out by the writer (77, p. 30) that while the tendency to aggregation may be the primary cause of reduction, the reduction would act as, at least, a partial cause in subsequent aggregation, and that there has probably been a continuous aggregation and reduction mutually interacting until the limit of efficiency has been reached.

Examples of the imperfect development of these two tendencies occur in the Lobelioideæ, Dipsaceæ, Valerianaceæ and Umbelliferae. The development along these lines has proceeded under the pressure of orthogenesis beyond the limit of full efficiency in quite a number of Composites, such as the dense aggregations of capitula, which are frequently few flowered, in the Gundeliinæ, Angianthinæ, Relhaniinæ, Echinopsidinæ, Lychnophorinæ, Lagasceinæ and Milleriinæ. It should be noted that these specialised sub-tribes are all shown to be end groups by the structure of the pollen-presentation mechanism (see Fig. 7, Chap. II).

C. DEVELOPMENT OF THE COROLLA.

For an account of the development of the complete floret the reader is referred to the previous publications discussed in Section A. The differences which characterise the mature corollas arise at an early stage. The difference in development lies in the behaviour of the two posterior petals. In the tubular corolla these two petals grow at the same rate as the others and remain in organic connection, as in *Senecio* (Fig. 9, 25, 26, 27), the mature floret showing a cross section, as in Fig. 9, 19. In the ligulate corolla

these two petals grow at the same rate as the others, but the organic connection between them ceases at an early stage, as in *Taraxacum* (Fig. 9, 31, 32, 33), the mature floret showing a cross-section as in Fig. 9, 21, with the free margins of these two petals closely adpressed. In the bilabiate corolla these two petals usually fuse at an early stage and then cease to grow, as in *Calendula* (Fig. 9, 30, 29, 28) the mature floret showing a cross-section as in Fig. 9, 20, with the free margins of the two lateral petals overlapping. In this type, however, the many variations in the degree of fusion and degree of development of these two petals give the various modifications described in Section B.

The primordial meristems are free at first in all cases giving five protuberances from the top of the primordium of the flower; these meristems then fuse to give a zone which is complete in the tubular corolla, interrupted regularly between the two posterior petals in the ligulate corolla, and interrupted regularly or irregularly in the bilabiate types. The development of the filiform corolla with 2-4 teeth at the apex has yet to be elucidated.

In ontogeny, therefore, as in phylogeny, the five-lobed tubular corolla is the primitive type, and from it arises two forms more distinct in their development than in their form when mature.

Causal Morphology—Experiments have been carried out along the lines of causal morphology as suggested by Lang (47) and although more or less unsuccessful may be of interest.

Apart from an internal modification of the constitution of the organism there are two factors which may influence the production of ray florets, pressure due to crowding of the florets in the bud and variation in food supply.

Taking pressure first, this factor is not a very probable one as in the development of the capitulum the rays are differentiated from the disc before the primordia have increased sufficiently to exert a pressure upon one another (see also Church, Pt. II, p. 114). They always mature late; the primordia of the petals in the ray are undeveloped when the first row of disc florets have the corolla, stamens and gynœcium differentiated.

Experiments on the influence of pressure were made by tying twine around capitula or placing elastic bands around them so that as they expanded in the later stages of development they were subject to a pressure from within outwards in the case of the twine and partly from without towards the centre of the capitulum where

rubber bands were used. Strong spring clips also were used to obtain pressure on two sides of the capitulum.

The material used was *Cotula coronopifolia* (a discoid species) *Ursinia speciosa*, *U. pulchra*, *Chrysanthemum Leucanthemum* (rayed species), and *Dimorphotheca pluvialis*; this last species had given numerous capitula with bilabiate corollas in the first and second rows of disc florets.

In no case did the treatment make any difference in the development of ray florets but in a few cases of *C. Leucanthemum* tied with twine the central florets of the disc were obviously crushed and failed to mature. The pressure in such a case arises from the expansion of the florets as it would in the case of the disc florets pressing the rays against the more or less rigid involucre.

The influence of the food supply was also investigated in *C. Leucanthemum* and *Dimorphotheca pluvialis*. This was done by cutting a notch halfway through the stalk of the inflorescence protecting the wound with vaseline and supporting the capitula. The results were again rather indefinite, but in the latter species the capitula so treated were rather poorly developed as a whole without much difference in the rays. In one case, however, there were five buds in different stages above the wound and, while the other peduncles of the same plant gave numerous cases with bilabiate disc florets, none of the capitula with deficient food material showed this modification, which involves a greater expenditure of material.

These results suggest that the factor for radiateness is probably a Mendelian one (see also Trow, 84) acting directly on the production of rays and not indirectly on the food supply or the amount of pressure developed by the disc florets. An abundance of food supply is suggested, however, as a contributory cause in the production of bilabiate disc florets and this explains, in part at least, the frequent production of "double" flowers by cultivated Composites.¹

D. VARIATION IN COLOUR OF THE COROLLA.

The phylogenetic value of colour as a character depends upon two chief points, our knowledge of the relation of colours and insects and our knowledge of the composition of the pigments. In

¹De Vries (87, p. 507) records warm weather as a factor in the production of "doubling" in the cornflower.

relation to insects all authorities are agreed that blue is the highest colour. The order of efficiency in attracting desirable insect-visitors may be taken as more or less established and beginning with green goes upwards through yellow to orange, white, pink, red, purple, violet and blue. Green, yellow, orange and white may be taken as the primitive group, and red, purple, violet and blue as advanced. The evidence as to the relative position of purple and blue was previously somewhat contradictory but the purely chemical evidence (95) serves to show that different colours, reds, blues and purples can be obtained by varying amounts of the same pigment, so that the Mendelian evidence of the duplex nature of purple is counter-balanced by the more recent additions to our knowledge of the second point.

Keeping the colour sequence in mind we can now analyse the colour of the corolla in the various groups:—

Senecioneæ—The predominant colour in this tribe is yellow, but orange, white, violet and purple occur in various groups of *Senecio*, which groups have been separated by several authors on this account. In the *Senecioninæ* blue occurs in *Cineraria*; orange and purple in two or three other genera; white is rare. In the *Othonninæ* blue, pink and white occur rarely, while in the *Tussilagininæ* white and purple become relatively commoner and in the *Liabinæ* white is the only colour except the predominant yellow. The *Senecioneæ* are, therefore, primitive in the colour, showing a marked predominance of the basal yellow and a range of colour in outlying genera and outlying species of the basal genus, *Senecio*. The higher colours are usually confined to the rays, the disc in these cases being almost invariably yellow.

Cichorieæ—Yellow is again predominant, white rare, orange, pink and red commoner. There is a sudden development of purple and pure blue occurs in several genera.

Calenduleæ—Yellow is again predominant in both ray and disc florets but more so in the latter. Three of the chief genera show orange in ray and disc sometimes and two of them, *Tripteris* and *Dimorphotheca*, show white and purple occasionally, the purple spreading to the disc in both genera.

Arctotideæ—Yellow is again predominant. In the *Arctotideæ* the basal genus, *Ursinia*, shows yellow in both disc and ray as a rule with purple rays occasionally. This purple spreads to the disc in *Arctotheca* and *Arctotis*; the latter shows a wide range in the rays with yellow, orange or purple in the disc. Orange occurs

in the disc of *Gazania* and purple in the rays of that genus and *Gorteria*. In the Gundeliinæ there is no yellow, only purple or violet, so that in the colour of the corolla we find confirmation of the evolution of these sub-tribes as given in Fig. 7, Chap. II.

Anthemideæ—Yellow is the predominant disc colour but white is common as a ray colour, and pink, red, purple and violet occur also. Yellow is more predominant in the Chrysanthemidinæ than in the Anthemidinæ, so that here we get the first indication of the relative position of these two sub-tribes.

Inuleæ—Yellow is the predominant colour for both disc and ray, higher colours, where they occur, frequently invade the disc. The relative positions of the Helichryseæ and Eu-gnaphalieæ are confirmed by the occurrence of white and purple in several genera of the latter, while purple is absent and white rare in the former. Blue occurs in *Printzia*, one of the Inulinæ. Yellow, orange and white are the only colours in the Bupthalthminæ, the only point in which the colour of the corolla does not confirm the arrangement of these sub-tribes in Fig. 7, but see below. Yellow is dominant in the other sub-tribes but higher colours up to purple occur occasionally.

Cynareæ—Purples and blues are characteristic, a dingy yellow occurs in *Carlina* and *Atractylis* in the Carlininæ, white and blue in *Echinops*; a distinct yellow occurs rarely in *Carduus* in the Carduinæ. These are the higher sub-tribes and in the Centaureinæ yellow occurs in *Centaurea*, *Carbenia* and *Carthamnus*, orange in the latter and in *Zoegea*. Yellow and orange are, therefore, comparatively well-developed in the sub-tribes placed at the base of the Cynareæ in Fig. 7. This fact and the predominance of yellow in the Bupthalthminæ are mutually explanatory in view of the derivation of the Centaureinæ from the latter sub-tribe.

Mutisieæ—The basal sub-tribe, Nassauviinæ, shows yellow commonly in three of the chief genera, *Trixis*, *Nassauvia* and *Jungia*, where it is associated with the lowest type of stamen in the sub-tribe. The other genera range from yellow to blue, the latter being rare, white, pink and purple, commoner. The Gerberinæ and Gochnatiinæ show a similar condition with blue absent, while yellow occurs only in *Mutisia* in the Onoseridinæ. The last sub-tribe might, therefore, be regarded as a side group with, perhaps the exception of *Mutisia*, where the yellow is associated with type IV styles and type 11 stamens. *Mutisia* would thus lead on to the Gerberinæ, giving the other genera of the Onoseridinæ as a special

development. Yellow is absent from the Barnadesiinae, but the presence of orange in *Schlechtendahlia* confirms the primitive position as in Fig. 7, Chap. II.

Vernoniae—Purple is predominant, with white, pink and red occasional, and yellow absent except for a greenish yellow in some species of *Corymbium* in the Vernoniinae.

Astereae—Yellow is again predominant in both ray and disc, especially in the latter. The chief point to be noted is the complete predominance of yellow in the Homochrominae as contrasting with the development of a wide range of colours up to blue in the rays of the Heterochrominae. These higher colours sometimes invade the disc, so that the relative position, as in Fig. 7, of these two sub-tribes requires to be reversed. A study of Tables VI and VII, Chap. II, shows that this can be done without inconsistency as the structure of the pollen-presentation mechanism in these two groups is very similar. The higher development of irritability (Chap. III, Sect. E) in the Heterochrominae is also explained by this change. As yellow is predominant in the Conyzinae and Baccharidinae these would retain their positions as coming from the lower of the two main groups, while the Grangeinae with purple and violet sometimes in the disc and yellow not predominant would retain its position as coming from the higher plexus. The Bellidinae with yellow as a constant disc colour and white, or rarely blue or purple, in the ray would remain near the base of the tribe, as a side group with its present development between the main groups.

Eupatorieae—Purple is predominant with white common. Yellow occurs only rarely in *Mikania*, which with *Eupatorium*, forms the basal group in the Ageratinae. Pink and blue also occur in a few genera.

Heliantheae—Yellow is predominant in both ray and disc especially in the latter. All the higher colours except blue appear occasionally, white being comparatively common in the ray, but the variation is so extensive that the position of the sub-tribes cannot be distinguished.

Helenieae—Yellow is again predominant but orange is frequent. White and purple occur but rarely in the Tagetinae, less rarely in the Heleniinae and Baeriinae. Yellow is the only colour in the Flaveriinae and Jaumeinae, so that the position of the former is confirmed and that of the latter above the Baeriinae is rendered

less probable. A study of Tables VI and VII shows that a lower position is possible and more data are required.

E. ANATOMY OF THE COROLLA.

For an account of the complete anatomy of the various types of florets the reader is referred to a previous publication (76) and the literature cited there. As the literature has already been discussed (Section A) it is necessary to give only a brief summary of the facts in their bearing on the general problem.

Tubular Corolla. There are five conducting strands which do not occupy the position of the midribs of the constituent petals but are situated along the fused margins (Fig. 9, 1). At or near the base of the corolla these strands, which originate in the upper distributive centre (see 76, p. 518), divide tangentially to give the staminal bundles. These pairs of bundles occupy the narrower part of the corolla, and the staminal bundles pass out into the filaments where these become free, usually at the base of the campanulate part of the corolla (cp. Fig. 9, 19).

The corolla strands continue upwards and divide radially at the bases of the corolla lobes. These half-bundles then arch over and fuse with adjacent halves, giving five arches along the margins of the five lobes. There is little or no variation in this type of corolla anatomy.

Ligulate Corolla. At the base of the corolla five strands arise from the upper distributive centre as in the above, but the behaviour of the posterior bundle is different. Near the base it divides, first tangentially to give the staminal bundle, and then immediately or a little higher up it divides radially to give two bundles which run along the margins of the ligule (cp. Fig. 9, 21 and 3). The other four bundles, some distance from the point at which they give the staminal strands, divide radially at the bases of the corolla lobes, bend over and fuse to give arches as before. The marginal bundles behave as the half bundles which they really are, and fuse with adjacent halves. The only real difference, therefore, between this and the tubular type of anatomy is that the radial division of the posterior bundle takes place earlier in the ligulate corolla. There is no recorded variation in this type of anatomy.

Bilabiate Corolla. The vascular supply of the bilabiate corolla varies with the width of the anterior lip as a rule, and the variations seem to be the result of a response to the physiological needs of

the corolla. Thus in the ray florets of *Tussilago Farfara* there are four bundles at the base of the corolla, the posterior one is short, while the two lateral strands end blindly in the tissue of the margin of the very narrow anterior lip. The one anterior bundle seems to be sufficient to supply the needs of the very narrow corolla. In the ray florets of *Calendula vulgaris* there are again four bundles, two small lateral strands occupying the margins of the anterior lip, and two larger strands occupying the fused margins of the anterior and two lateral petals (Fig. 9, 2). These form arches at the top of the corolla as in the previous types. The *Calendula* type may be taken as the usual one for a ray floret, but there are many variations. The anterior lip may be four-lobed with five bundles (two marginal), or it may be broad and three-lobed with a vascular supply for four lobes, or it may be narrow and two-lobed or entire with a vascular supply for three lobes, *i.e.*, four bundles with two marginal.

Where the anterior lip is broad the strands tend to increase in number, the accessory strands frequently developing in the positions of the midribs of the three petals, giving a total of seven. The number in the wider part of the lip is frequently increased to twelve and more by branching of the four primary strands or of the three midribs. Usually these accessory strands end blindly in the tissue of the corolla, only the primary strands fusing to form the marginal arches at the tip, but fusions of various kinds may take place.

According to a figure by Hildebrand (36, Plate V, Figs. 22-23) the vascular supply of the irregularly bilabiate corolla in *Centaurea montana* is similar to that of the tubular corolla with the radial divisions occurring at irregular heights.

The known facts are, therefore, that the anatomy of the tubular and ligulate corollas is constant, and that of the bilabiate corolla is as variable as the external form of that type.

F. PHYLOGENETIC SIGNIFICANCE OF THE COROLLA.

When all the foregoing facts concerning the corolla are considered they are found to confirm the previous phyletic suggestions in all except a few points.

The primitive nature of the tubular floret, which is shown clearly by Uexküll-Gyllenband (Fig. 4, Chap. II) is confirmed by the study of the development and vascular anatomy of the corolla and the various lines of evolution shown in Fig. 4 follow comparatively closely the scheme in Fig. 7.

The distinction between the ray florets of several tribes and the bilabiate florets of the Mutisieæ is removed, making it more probable than ever that the latter tribe is a mere collection of bilabiate forms and not a natural tribe.

The occurrence of many discoid forms and the predominance of yellow in the Senecioneæ confirms that group as the basal plexus. The similarity in colour and the small change in the form and anatomy of the corolla in the Cichorieæ confirm the position of that tribe. The similarity in form and colour of the corolla in the Calenduleæ confirms the position of this tribe. The greater predominance of yellow in the Chrysanthemidinæ suggests that this is the more primitive sub-tribe in the Anthemideæ.

The colour and form of the corolla in the Vernoniæ and Arctotideæ confirm the positions of the sub-tribes in these two groups, and the yellow of *Ursinia* adds evidence for the suggestion that that genus is the primitive one in the Arctotideæ. The frequent disappearance of the ray florets in many tribes makes the origin of the Vernoniæ from a rayed group like the Liabinæ very probable, and the occurrence of several discoid genera in the Liabinæ confirms that sub-tribe as the source of the Vernoniæ. Indeed, *Gongrothamnus*, one of the Liabinæ according to Bentham, is placed in the genus *Vernonia* by Hoffmann.

The occurrence of filiform florets in the lower sub-tribes of the Inuleæ and in a few genera of the Astereæ is accounted for by the plasticity of organisation proved for the outer florets of the capitulum. The occurrence of the same type in *Homogyne* (Tussilagininæ) shows that the tendency towards the reduction of the bilabiate corolla to the filiform type is already present in the Senecioneæ, finding expression in two separate lines of evolution. The rayed condition in the higher Inuleæ may be regarded as a reversion to the general type, but it is possible that this tribe is not monophyletic but diphyletic, in which case the Cynareæ may have arisen either from the Bupthalthinæ as previously suggested, or from the Plucheinæ through forms such as *Cavea* (74a). Other data are required to elucidate this point.

The derivation of the Cynareæ from the Bupthalthinæ is partially confirmed by the colour, yellow in a few Centaureinæ and in the parent sub-tribe. The relative positions of the sub-tribes of the Cynareæ are also confirmed by the distribution of colour in the tribe.

The derivation of the Nassauviinæ from the Senecioninæ is confirmed by the bilabiate corolla which occurs in *Brachyglottis* (cp. Fig. 10, C-D), and by the predominance of yellow in the chief genera of the former sub-tribe. The spreading of the bilabiate condition to the disc is quite homologous with the "doubling" which is of such frequent occurrence throughout the family, probably under the influence of an abundant food supply. The transition from the more or less homogeneous capitulum of the Nassauviinæ to the forms with only several outer rows of bilabiate florets is seen in the genus *Mutisia*, which also shows a transition to the higher colours. The other genera of the Onoseridinæ appear both from the form and the colour to be a special development, *Mutisia* itself giving rise to the Gerberinæ. With this change both form and colour confirm the evolution of the sub-tribes as given in Fig. 7.

In the Astereæ it is clear from the colour relations of the sub-tribes that the relative positions of the Homochrominæ and Heterochrominæ must be reversed, as suggested in Chap. III, Sect. E, the other sub-tribes remaining as they are in Fig. 7. As the degree of development of the pollen-presentation mechanism in the two sub-tribes is very similar this can be done quite conveniently without disturbing the relationships of the other sub-tribes. We then get the yellow Homochrominæ giving the Heterochrominæ with the higher colours appearing first in the rays and then spreading to the disc. The filiform corolla appears more or less sporadically and can be interpreted as the expression of a tendency to reduction which reaches its highest development in these same genera.

The spreading of the higher colours to the disc is a step towards the development of the discoid, highly coloured capitula of the Eupatorieæ, which show higher colours as a rule, yellow appearing seldom, and then only in the basal group of the tribe. The disappearance of the ray florets is a normal phenomenon throughout the family.

There is a great similarity in both form and colour in the Heliantheæ and Senecioneæ, but the higher colours are more frequent in the former tribe, thus confirming its position above the Senecionineæ. The relative positions of the sub-tribes in the Heliantheæ are neither confirmed nor refuted on account of the great variation shown in both form and colour.

The derivation of the Helenieæ from the Heliantheæ is confirmed by the similarity in form and colour, but the complete

predominance of yellow in the *Jaumeinæ* renders the position of that sub-tribe above the *Bæriinæ* less certain. It could be regarded as coming direct from the *Tagetinæ*.

With a few modifications, therefore, the study of the form, development, colour and vascular anatomy of the corolla confirms the phyletic lines previously suggested.

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CHAPTER V.

THE PAPPUS.

THE matter in the previous chapters has not been controversial to any marked extent. Any controversies which there have been, such as those on the venation of the corolla and on the function of the hairs on the styles, are now dead, but the question of the phyllome or trichome nature of the pappus is still in dispute. The evidence which has been previously adduced is, therefore, given in some detail in Section A, and additional facts, which help to present the matter in a new light, are brought forward in Section B. The whole of the fruit might have been considered in this chapter but as the structure of the fruit, apart from the achenial hairs and the pappus, seems to have little or no phyletic¹ value, (cp. Lavialle, Chap. I, Sect. B), it is omitted from the present discussion. As the question of the use of the pappus in fruit dispersal seems closely allied to the subject of geographical distribution it, also, is omitted and will be considered in a later chapter.

A. HISTORY.

Morison (52) was one of the first to use the presence or absence of the pappus as a character for the sub-division of the family; Ray (57) and others followed. Vaillantus (67) distinguished three types, pilose, plumose and coroniform. The aculeate or aristate type was added by Boerhaave (7) and the squamose or paleaceous type by Pontedera (55), who also distinguished the "corticose" fruit of *Calendula* and the "osseous" fruit of *Osteospermum*. Forty years later Berkhey (6) gave some figures of the various types and enumerated the coroniform, pilose, plumose, sessile and stipitate types. Gaertner (20) in his special study of fruits made some advance, distinguishing foliose, capillary, setose, plumose, spiny, penicillate and aristate forms.

The details of the various types of pappus, like most other floral details in the Compositæ, were most fully developed by Cassini (11, 4th Mem.). Thereafter these data were applied in all taxonomic systems.

¹ The biological or economic value may, of course, be considerable, e.g. the mucilaginous pericarp in many species (14), and the use of sunflower fruits as a source of edible fats.

The Cichoriæ being such a uniform group, the pappus here has received special attention. Cassini (11, Tome I, p. 380) used the pappus with other characters of the fruit, and Don (15) also used the pappus with other characters in his classification of the Cichoriæ. De Candolle and Bentham followed Cassini; Hoffman (34) suggested a very simple but very artificial classification on the coroniform, plumose or pilose pappus but this was rejected as already mentioned (Chap. I, Sect. A) by Engler and Gilg (18).

Taxonomic Value of the Pappus.

The above is one example of the use of the pappus in taxonomy. As usual the use of only one character gives a very convenient but unnatural grouping. Another example is the importance attributed to this part of the fruit by Hutchinson (37 and 39) and his use of the presence or absence of the pappus in the separation of *Brachymeris* and *Marasmodes* (37). This author considers the pappus "one of the most important features in the consideration of the phylogeny and affinities of the genera of this interesting family." In accordance with this view he takes the absence of the pappus with the absence of glandular pits from the leaves as forming a difference of generic value (*loc. cit.*).

In contradistinction to the views of Hoffman and Hutchinson we have Bentham (5, p. 354) on the pappus as follows: "it is on the ripe achene that it has attained its fullest development in those innumerable variations which strike the eye of the most superficial observer, and which have been eagerly seized upon to characterize a large proportion of the thousand and one petty genera with which syantherology has been encumbered. Constant or nearly so in each species, with very few exceptions, the pappus will often, in a most natural genus, so vary from species to species as to make it a most difficult task to decide whether it should be neglected altogether, or, if taken into account, what modifications may be taken as generic, sub-tribual, or tribual. The presence or absence of a pappus or its degree of development is always of much less importance than its nature when present." As a result of the analysis of the pappus forms given below the writer is of a similar opinion.

The new genera, *Triplotaxis*, Hutchinson (36) and *Cavea*, Smith and Small (62) are examples of the value of the structure of the pappus when present, but the case of *Bidens* and *Coreopsis* makes an interesting commentary. *Bidens* is characterized by downwardly projecting barbs on the aristæ of the pappus; *Coreopsis* is distinguished from *Bidens* merely by the upwardly projecting

barbs, but *Coreopsis aristosa*, Mich. is described (23) as having no pappus at all or aristæ with downwardly or upwardly directed bristles. These forms abound in the same locality and the probability of hybridisation is negated by the absence of *Bidens* from the districts where these forms occur.

Dispersal Mechanisms.

Hildebrand (30) considers the pappus at some length in its relation to dispersal by wind and by animals. In his general memoir (32) also he gives figures and details of a number of hooked and pappose fruits in the Compositæ having previously developed the subject of dispersal by hooks in a special contribution (31). Hooked fruits in the Compositæ are also considered by Huth (41). Yapp (71) and others have described various Composite fruits in which the pappus is glandular and sticky.

The presence of a pulvinus at the base of the pappus either in the form of a ring or isolated at the base of each seta has been noted by Schenk (59), Taliew (65), Haberlandt (22), Hirsch (33), Steinbrinck (64) and Yapp (71).

Taliew distinguishes three types of mechanism for the spreading of the pappus in dry conditions, I—the *Lactuca* type with an annular pulvinus, II—the *Tussilago* type with no pulvinus but unequal thickening of the pappus hairs, III—the *Cirsium* type with a pulvinus to each seta. The first type was recorded by Schenk and Taliew in all the Cichoriæ and most of the Tubulifloræ examined. The second type in which each seta curves on drying occurs chiefly in the Tussilagininæ. The third type is characteristic of the Cynareæ, and experiments by the writer show that in the case of *Centaurea imperialis* the mechanism is very sensitive to the degree of the humidity of the atmosphere. With a Relative Humidity of .78 the pappus remains closed, or, if opened by drying in a warm test-tube, closes rapidly when brought into the air. With the R. H. .77 it remains open for some time after previous drying and with the R. H. .75 it opens spontaneously and remains spread at an angle of 45° for an indefinite period.

There are various other contributions to this part of the subject but they are concerned more directly with fruit dispersal and will be dealt with in a later chapter.

Pericarp Structures.

Capus (10), Hanausek (24-25), Portheim (56), Lavielle (45) and Loose (46) have recorded the detailed structure of the pericarp in

many genera. The phylogenetic results obtained by Lavialle have been mentioned already (Chap. I, Sect. A, and Fig. 3). In addition he gives a very complete summary of our knowledge of the fruit in the Compositæ, dealing with the ovule, epithelium of the embryo sac, the haustorial function of the antipodal cells and other matters, which may have a certain phyletic value but which are outside the scope of the present chapter.

Joxe (42) gives details of the various types of germination in the Compositæ, some of which are quite aberrant. Hanstein (27), Haberlandt (22) and Yapp (71) mention the capitate hairs which are so characteristic of certain genera, notably *Helianthus*, *Calendula* and *Inula*.

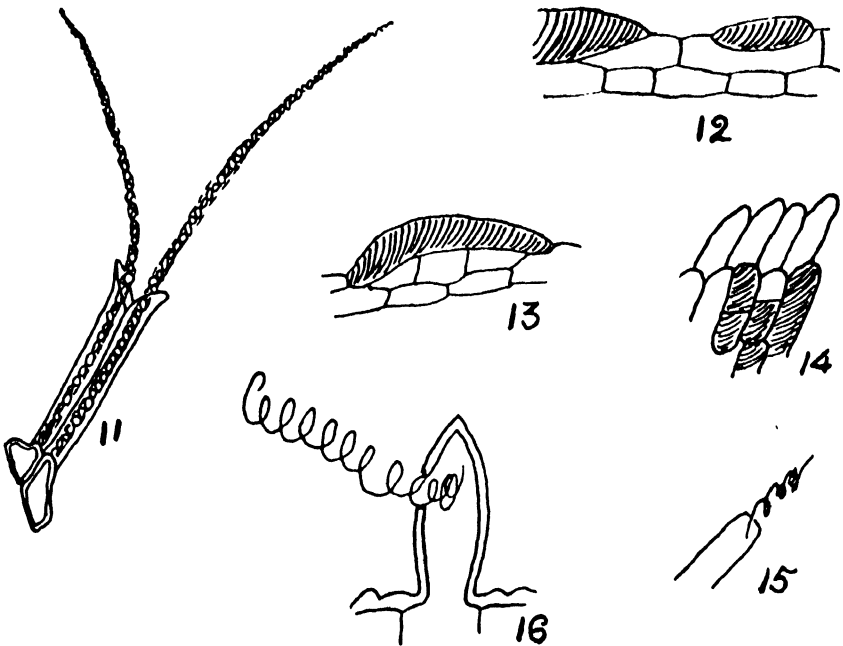
Achenial Hairs.—The most interesting part of the pericarp from the present point of view is, however, the hairs which occur on very many of the fruits. These were studied in detail by Macloskie (49), and, as they appear to be of considerable phyletic value, they will now be considered in some detail. The curious duplex hairs of the cypsela of *Senecio vulgaris* have long been objects of interest. They are situated in the furrows between the ridges of the pericarp, and are composed of two cells placed side by side, each containing a spiral fibre, which on being moistened swells and shoots out at the top of the cell, showing movements like those of the elaters of the liverworts. This double tube is mounted on a pedestal of two clear cells (Fig. 11).

Archer (1) and Kraus (44) mention these duplex hairs as common in the Compositæ. Macloskie examined genera from most of the tribes, and says "the consideration of the facts stated above suggests a somewhat different line of affinities from that usually adopted." He did not, however, make any definite phyletic suggestion. Harz (28), Heineck (29), Nichols (53) and Lavialle (45) extended the observations, but again drew no definite phyletic conclusions, so that we are free to make what use we can of the facts.

The duplex hairs with elaters are characteristic of the Senecioneæ, similar duplex hairs with acute tips and no elaters, occur in the Astereæ, Eupatorieæ, Vernoniæ, Heliantheæ, Heleniæ and Arctotideæ. The Anthemideæ have no such hairs but cells with spiral filaments occur on the outside of the pericarp in certain cases (Figs. 12-13).

The Calenduleæ are probably similar to the Senecioneæ according to Macloskie, with the addition of the above-mentioned capitate hairs. The cypsela of the Cichorieæ is glabrous but

shows denticulate epidermal cells, and below these in many cases cells with spiral filaments (Fig. 14).



ACHENIAL HAIRS OF COMPOSITÆ.

FIG. 11. Duplex hair of *Senecio vulgaris*; Fig. 12. Elater cells of *Chrysanthemum Leucanthemum*; Fig. 13. Ditto of *Maruta Cotula*; Fig. 14. Endocarpal filaments and denticulate epidermal cells of *Lactuca scariola*; Fig. 15. Endocarpal fibril of *Cirsium lanceolatum*; Fig. 16. Elater cell of *Trixis*. Figs. 12-15. after Macloskie, Fig. 16 after Laviolle.

The Cynareæ vary; some have duplex hairs as in the Astereæ, others have simple hairs, and others again show endocarpal filaments as in the Cichorieæ (Fig. 15). *Centaurea* shows simple hairs. The Inuleæ have duplex hairs similar to those of the Astereæ but with obtuse tips. In view of the suggestion that *Cavea* (Plucheinæ) is an intermediate type between the Inuleæ and Cynareæ (see Chap. IV) it is interesting to note that the typical Asteroid hairs occur in *Pluchea foetida* (Plucheinæ) as well as in the Cynareæ.

One of the most interesting points is the variation in the genus *Trixis* of the Nassauviinæ. According to Laviolle (op. cit.) *Trixis Lessingii*, *T. verbasciformis* and *T. mollissima* have one or two-celled simple hairs, but *T. pallida*, *T. Hieronymi*, *T. ochroleuca* and *T. brasiliensis* have simple hairs with spiral elaters (Fig. 16). If this is read in connection with the suggestion of *Trixis* as the primitive genus in the Nassauviinæ (see below, Sect. C.) the phyletic value of these hairs becomes obvious.

If the *Senecio* type of duplex hair be taken as primitive, it is clear that it has passed through several forms of reduction along the various lines of evolution suggested in Fig. 7, Chap. II, the elaters disappearing more or less in the Inuloid, Helianthoid and Asteroid lines, the hairs becoming reduced to single elater cells in the Mutisieæ or to short external cells in the Anthemideæ and, perhaps, passing below the epidermis in the Cichorieæ. It is doubtful, however, whether the endocarpal filaments in the Cichorieæ and Cynareæ are homologous with the elaters.

Development.—Before Buchenau published the first complete account of the development of the floret in 1854 (8a), Duchartre (16) had recorded some observations on *Helianthus*, from which he concluded that the two paleæ on the top of the cypsela were epicalyx leaves or bracteoles, fused with the ovary for part of their length; the calyx he considered to be completely fused with the lower part of the corolla tube. Duchartre also regarded the pappus in *Bidens* and all paleaceous pappi to be of a similar epicalycine nature.

In subsequent observations apart from the phyllome or trichome nature of the pappus, the chief point recorded is the origin of that structure after the corolla and stamens have been differentiated, see Chap. IV, Sect. A, and the literature there cited.

An isolated but interesting observation is that by Baart de la Faille (2), who, as an example of his thesis that logarithmic distribution is more frequent in nature than the normal curve, takes the top cells of the pappus in *Senecio vulgaris*, and shows that any increase in length is directly proportional to the length already acquired.

Phyllome v. Trichome.—The question of whether the pappus in the Compositæ is a modified calyx-limb or merely hairs or emergences on the top of the so-called calyx tube is still a question of controversy, the latest contributions dating from 1916.

The controversy reached its height about 1873, but Richard (58) had previously stated that the pappus had been recognised for a long time as analogous to the calyx of other families. He adds as a caution “néanmoins ce seroit une grande erreur d'assimiler en tous points l'aigrette aux calices ordinaires.” Cassini (11, Tome I, p. 202) describes the pappus as “un calice épigyne, d'une nature particulière” and analogises it (op. cit., p. 219) with the paleæ of the receptacle and with the involucre bracts. His argument is “ces paillettes et ces écailles sont incontestablement des bractées.

Donc l'aigrette est un assemblage de bractées, lesquelles sont disposées à peu près celles des calices ordinaires ; donc l'aigrette est un calice." This is typical of much of the loose and superficial reasoning on the subject. On p. 273 (op. cit.) he evidently takes the squamellules of the *Cynareæ* as bracts, cp. below, Sects. B-C.

Kohne (43) supported the phyllome theory on account of the insertion of the setæ in several genera at five points, after the manner of the pentadelphous stamens in *Hypericum*. The setæ were, therefore, regarded as divided calyx leaves, while Cassini and others regarded them as single sepals and the calyx as having undergone *dédoublement*.

Buchenau (8b) is quoted by Masters (51) for the trichome theory and by Lund (47) for the phyllome theory. This is because he at first supported the former theory and then partially withdrew in the paper quoted. He definitely states that there is a calyx, and then goes on to show that the pappus hairs and scales are accessory organs of the semi-aborted calyx and not organs of the same importance as the other appendicular organs of the flower. He quotes cases where a pappus was observed inserted on five or more green leaflets which were provided with vascular bundles and developed in inverse proportion to the pappus.

Lund (47) maintains that the pappus must be of a phyllome nature, each seta being a sepal, because in *Cirsium* and other genera vascular bundles of a more or less rudimentary nature are present in the paleaceous setæ. According to Lund (op. cit., p. 259) "l'aigrette des Composées est un véritable calice." This same opinion is expressed by Treub (66) as a result of finding all stages in the passage from the normal pappus to five free leaves with vascular bundles in the galls which sometimes occur on the capitula of *Hieracium umbellatum*.

Bentham (5, pp. 354-5) repeatedly mentions the fact that the pappus is generally regarded as a reduced or modified calyx-limb, but he remained non-committal on account of the many variations with which he was familiar. He says "their homology is not so easy to settle," and again, "the occasionally present, reduced, innermost row . . . may only be a modification of the epigynous disc."

Eichler (17) gives a full account of the controversy to his date 1875, quoting Hofmeister (35) and others as regarding the pappus as an isomerous, oligomerous or pleiomerous true calyx, and further authorities for the trichome or emergence nature of the organ.

Eichler considered both these views wrong and regards the pappus as a modified calyx. He quotes the cases with a reduced number of paleaceous setæ as proving the leaf-nature of the pappus (cp. below, Sect. B).

Coulter (12) and Martin (50) consider the pappus as a calyx, the liberation of the upper part being retarded in the development of the flower. Worsdell takes a new line of argument (69, p. 954), "if the pappus is not the homologue of the calyx, where are we to look for the latter in the normal floret? for it cannot be supposed to be entirely absent." Baillon (3) had previously stated that in the case of *Xanthium* there is nothing in the flower at any age which represents a true calyx. Worsdell (70, p. 77) considers that a pappus may also arise from supernumerary petals, as in the *Leontopodium alpinum* β *nivale* observed by De Candolle (9), and also states (70, p. 66) that "normal examples of the multiplication of sepals are seen in the pappus of the Compositæ." Hutchinson (39) follows Worsdell.

Warming (68) pointed out that the pappus hairs could not be sepals because they do not occur in the position of sepals, and because they have a function usually attributed to hairs. He regarded the pappus hairs as "epiblastemes" which differ essentially from the more highly organised "epiblastemes" and considered that the true calyx of the Compositæ is the slightly developed annular ridge at the top of the cypsela from which the pappus hairs arise. The rudimentary vascular bundles on which Lund laid so much stress are considered by Warming to be of little importance.

A similar view was held by Hänlein (26) and Masters (51). The latter answers the teratological arguments of Treub and Worsdell, when he points out that "the occasional development of an organ which is usually suppressed does not prove that the parts that are generally present, like the pappus, are necessarily modified representatives of abortive organs." Taliew (65) states as an accepted fact that the setæ have the character of emergences in all the types examined by him. McNab (48) in reviewing Lund's work considers that, although in some cases the pappus scales may be sepals, "in the majority the scales or bristles or hairs of the pappus are undoubted trichome structures."

Such is the controversy in which the two chief British teratologists disagree in the most decided way, in which more or less detailed observations of a limited number of species are used to support the phyllome theory, while the general and well-known facts

of structure and position are used to support the trichome theory. The view adopted in most text-books is that of Richard and Eichler that the pappus is a modified calyx limb, but it seems to the writer that Goebel's argument (21, p, 317) concerning the nature of the receptacular setæ is quite applicable in this case also. It runs as follows—"Where now instead of single parts of a hypsophyll we see 'bristle-scales,' a qualitative change has taken place which may have begun with a transformation of the single parts of the hypsophyll, but I see no ground even then, if the hypsophyll no longer exists, for keeping its ghost hovering above, or rather below, these bristle-scales; to assume that it still exists is an 'idea,' and this 'idea' is stuck somewhere in the axis and allows only the bristle-scales to appear. Such 'ideas,' however, are to be found even in recent botanical literature."

This may be applied with more appropriateness on account of the evidence given below for the primitiveness of the setose pappus within the family and the compound setose character of even the reduced number of paleaceous structures so frequently quoted as being very similar to a true calyx.

B. STRUCTURE OF THE PAPPUS.

When we examine the actual structure of the various types of pappus most of the difficulties connected with the trichome and phyllome theories disappear. We must, however, be content to regard the pappus as a structure more or less *sui generis* as advised by Richard.

As with the styles and stamens we can reduce the innumerable variations to a limited number of mean types which pass gradually into one another. These mean types will now be described briefly. The fundamental type is the scabrid seta, composed of uniseriate rows of cells fused together, with the obtuse terminal cell of each row free and projecting outwards as a lateral cilium for a distance which is less than the diameter of the seta. This is described as *setose scabrid* or *setose denticulate* (Fig. 17, A). That the structure is a fusion of uniseriate hairs such as are common on the cypsela is obvious and really requires no comment.

There are various modifications of this basal type; if the ends of the constituent hairs do not project the seta is simple, as in *Tussilago*, and the upper part may be unicellular in cross-section as previously mentioned (61). This is described as *simple setose*, (Fig. 17, B). The projecting lateral cilia may be acute and arranged in a

serrate fashion, then the pappus is described as *setose serrulate*, (Fig. 17, C). If the lateral cilia are as long as or slightly longer than the diameter of the seta, the pappus is described as *setose barbellate*, (Fig. 17, D). This form leads on by the elongation of the lateral cilia to the *setose plumose* type, (Fig. 17, E), where the projections are considerably longer than the diameter of the seta.

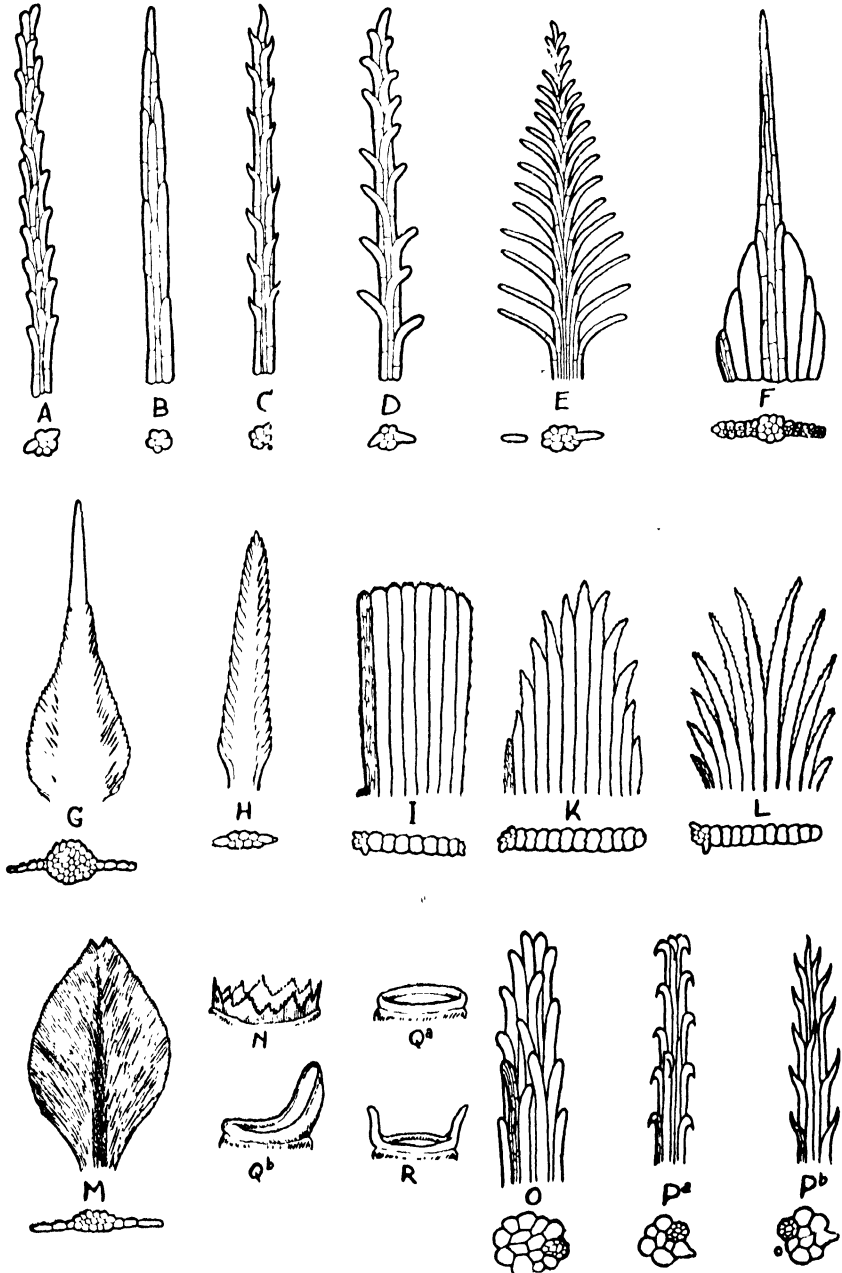
Setæ of these various types occur in large numbers, in one or two or more rings on the top of the cypsela, and there is no commoner modification than the fusion of the setæ at the base, to form a more or less continuous membranous collar of tissue. This modification is quite in harmony with the tendency to reduction and cohesion present in other floral members. It is duly noted by Hoffman (34) in his non-committal description of the various modifications of the pappus. It is included in many descriptions of species, such as *Vernonia Kerrii* (13), and is frequently a character of generic rank. It occurs in the sub-genus of *Senecio*, *Senecillis* (19). It was noted in *Tussilago* by the writer (61) and occurs in a very large number of genera.

This being the case it is not surprising to find that sometimes the collar is discontinuous and broken up to give a number of scales, paleæ or squamellæ. The setæ frequently vary in length, so that fusion gives a form described as *paleaceo-setose* (Fig. 17, F). The paleaceous part may be comparatively short or relatively long on the same fruit. The addition of one or more setæ to the central rib or the further thickening of the single central seta gives a similar type, which is usually ciliate at the edges, as in *Gaillardia*, and is known as *aristato-paleaceous*, (Fig. 17, G). By a slight elongation and a crowding together of the lateral cilia, as in *Centaurea calocephala* (22, Fig. 220. p. 545), we get a *serrulato-paleaceous* form (Fig. 17, H). If the constituent setae are of equal length and fuse completely a *simple paleaceous* type (Fig. 17, I) results.

It may be rather surprising that this simple fact of the trichome nature of the paleæ has not been more widely recognised. Anyone can mount the simple paleæ of *Berkheya* or *Tagetes* and see with oblique illumination under the low power of a compound microscope that the facts are as stated. The free ends of the constituent hairs can be seen distinctly and the ribbed surface is obviously formed by the fusion of the constituent setæ.

If the ends of the setæ are free to a slight degree the result is a lacerate margin, giving the *fimbriato-paleaceous* type, (Fig. 17, L).

The plumose seta by the fusion of the lateral cilia in the same way as in the *serrulato-paleaceous* type gives rise to the *plumoso-paleaceous*



PAPPUS-FORMS IN THE COMPOSITÆ.

FIG. 17. Below each figure of the surface view a transverse section is given in most cases. The individual setæ are outlined by heavy lines; the constituent hairs are indicated by thin lines, in some cases only in part for clearness.—A. setose scabrid; B. simple setose; C. serrulato-setose; D. barbellato-setose; E. plumoso-setose; F. paleaceo-setose; G. aristato-paleaceous; H. serrulato-paleaceous; I. simple paleaceous; K. fimbriato-paleaceous; L. setoso-paleaceous; M. plumoso-paleaceous; N. fimbriato-coroniform; O. aristate; Pa-Pb. barbato-aristate; Qa. coroniform; Qb. auriculato-coroniform; R. aristato coroniform.

type, (Fig. 17, M), with a structure very closely resembling that of a feather. This occurs notably in *Ursinia*; the paleæ here make very pretty objects under oblique illumination and the structure is quite apparent even to the uninitiated.

As mentioned above, the setæ are frequently more or less connate at the base, and by the abortion of the free parts we get another common form, the *fimbriato-coroniform* type (Fig. 17, N).

In these paleaceous forms the setæ are fused laterally with one another, but they may also fuse in a clump, when a thick, more or less rigid structure arises, which is known as *aristate* (Fig. 17, O). The free ends of the setæ are usually blunt and project to a slight extent, but each seta may end in a large, strong, acute bristle. This type is described as *barbato-aristate*, and the bristles may project downwards, as in *Bidens* (Fig. 17, P^a), or upwards, as in *Coreopsis* (Fig. 17, P^b). These aristæ are frequently few in number, as one would expect when it is remembered that a number of setæ go to form each one.

Just as the paleaceous types by extreme reduction give type N, these aristate types by fusion and reduction may give a thick, cartilaginous ring at the top of the cypsela, which is described as *corneo-coroniform* (Fig. 17, Q^a). This ring may grow out on one side to form an ear-shaped or *auriculato-coroniform* pappus, (Fig. 17, Q^b). The auricle may be simple or lacerate like type K, e.g., *Pentzia* (see 38, Plate X). Finally by a similar reduction we may get two horn-like projections (Fig. 17, R).

Evolution of the Pappus-forms. Most of the evolution of the various types of pappus is obvious, but a diagram (Fig. 18) is given for convenience. The setose-scabrid type is taken as primitive and by fusion at the base with subsequent reduction gives type N. This *fimbriato-coroniform* type, like the simple paleaceous type, I, is clearly polyphyletic and may be derived easily from a number of types such as B, F, L and K. The evolution of the *serrulato-paleaceous* type, H, is clearly through type C. The various steps towards, or the direct evolution of types F, I and M are indicated, and the various types arising from the aristate type, O, are arranged so that downward lines are lines of reduction and upward lines are lines of progressive differentiation.

The inter-relationships and possible evolutionary connections of the various types are somewhat more complex than in Fig. 18, but it is considered unnecessary to complicate the matter further since alternative methods of evolution of such types as F, G and M.

will be obvious to the reader. The main point is that the setose type is primitive and the paleaceous, coroniform and aristate types derived.

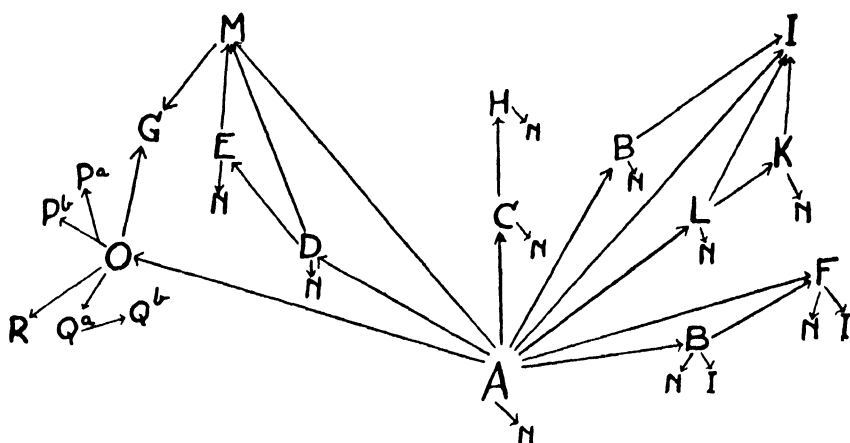


FIG. 18. Evolution of the Pappus-forms in the Compositæ.

The origin of the plumoso-setose type from the barbellato-setose type has been previously noted by the writer (62). The origin of type N from type K is a very obvious explanation of the well developed fimbriato-paleaceous pappus described by Békétóff (4) in an anomalous *Cichorium Intybus*. The origin of type N from type P explains the frequent mixture of short lacerate squamellæ with a few awn-like, elongated squamellæ, as in *Helianthus scabra* (54). Similarly the origin of the aristæ, by the fusion of setæ explains the frequent variation in the number of aristæ, even in a genus such as *Bidens*, where they are an important diagnostic character, but in which the aristæ vary from two to ten (60).

It is clear from the above details that the primitive pappus in the Compositæ has a trichome structure, whatever its homologies may be, and that the foliose calyx limb, when it occurs teratologically must be regarded as a reversion to a pre-Composite ancestor. It will be shown in a later chapter that there is every reason to believe that the Compositæ were derived from genera such as *Siphocampylus* in the Lobelioideæ, in which the calyx limb is frequently very much reduced or even (as in *S. eximius*) altogether absent.

Where a calyx limb is present in addition to numerous hairs of various kinds showing similar modifications to those of the pappus, as in *Triumfetta* (93, and see also 32), there has as yet been no suggestion of homologising the hairs of the fruit with the calyx limb. Masters' argument that the absence of one set of organs is no proof

of the nature of another set which is present, seems to the writer very appropriate.

The five-point insertion of the setæ and the frequency with which five or ten occurs as the number of paleæ or aristæ is quite explicable by the simple physiological fact that the food supply is naturally greatest near the five or ten vascular bundles which supply the ovary wall in most genera. As these bundles also supply the margins of the petals it follows that the paleæ and aristæ, when five, alternate with the petals and thus develop in the position of sepals.

Thus the application of a little microscopy combined with an obvious application of elementary physiological facts removes the clouds of controversy and lays "the ghost of the hypsophyll" which troubled Goebel.

C. ANALYSIS OF THE PAPPUS-FORMS.

Having determined the structure and evolution of the various mean types of pappus we can now analyse the distribution of these types throughout the family, taking the tribes in the order which is suggested by other phyletic data. As the pappus shows great variety, sometimes even in the same genus, it will be necessary to consider the tribes in some detail.

Senecioneæ. In the basal genus, *Senecio*, the pappus is usually copious and setose scabrid, but it varies to simple setose and is sometimes barbellato-setose, or of fewer, thicker, almost aristate setæ, which may be paleaceous at the base, as in § *Senecillis* (= *Ligularia glauca*, Hoffm.), or the scabrid setose type may be paleaceous at the base, as in *S. Grahami*, Hook. It may also be reduced to very short setæ or may be altogether absent.

The closely related genera, *Culcitium*, *Gynura*, *Cineraria*, *Emilia* and *Gynoxys* are all setose scabrid or barbellato-setose with the setæ in one, two or more rows as in *Senecio*. The genus *Raillardia*, which Hoffman removes to the Heliantheæ, and *Raillardella* are plumoso-setose. The other genera are all setose scabrid.

In the Tussilagininæ the simple setose type occurs in *Tussilago*, but the other genera are setose scabrid or barbellate. All the Othonnininæ and most of the Liabinæ are similar but in some species of *Liabum* an outer row of short, fimbriato-paleaceous scales occurs. In the Senecioneæ, therefore, all the primitive types, A, B, D, E,

L, K, and O, occur (cp. Fig. 18). Of these primitive types the lower forms, A, B, D and O, occur in *Senecio*.

Cichorieæ. The pappus here may be absent or reduced to the fimbriato-coroniform type; usually, however, there are one, two or more rows of scabrid setæ. In *Tragopogon* and its allies the setæ are usually plumose, frequently very elaborately so, with the primary and secondary cilia forming a network. The setæ are frequently connate at the base and deciduous, either singly or in a ring if connate.

In *Cichorium* there are two or three rows of short, connate paleæ, giving type N, but in allied genera the paleæ are fewer, longer and fimbriato-paleaceous, sometimes prolonged into awns as in type G, sometimes, as in *Hymenonema*, there are numerous barbellate setæ in the external rows and fewer sub-paleaceous setæ in the inner rows. This duplex or triplex pappus, apparently foliose in one row and setose in others, is very difficult to explain by the phyllome theory but has a quite simple and obvious explanation if the fusion of setæ is a "critical tendency," as advocated in Section B. A transition to the corneo-coroniform type occurs in *Koelpinia*, where the aristæ are short and connate at the base.

Calenduleæ. Setæ are rare in this tribe; *Dipterocome* has five to ten setæ with the addition of two appendages of type R and a few species of *Osteospermum* have one row of scabrid setæ. In the other genera the pappus is either absent or of types N or Qb.

Arctotideæ. According to the previous data *Ursinia* is probably the basal genus here. The pappus of that genus is composed of five paleæ of type M. The compound setose character is obvious as mentioned above and it will be noted that type E occurs in the Senecioninæ. In addition, however, a few setiform paleæ of type F or G are sometimes present as an inner row, so that we have the complete series of allied forms in this genus and the sub-tribe from which it is suggested to have arisen. In the other genera of the Arctotidinæ the paleæ are usually numerous, types I or K; type F occurs in *Haplocarpha*, a modified combination of types N and Qa in *Cryptostemma* and numerous paleæ of type I in *Arctotis*. The pappus is absent in a few genera.

The chief genus in the Gorteriinæ is *Berkheya*, which has a pappus essentially similar to that of *Arctotis*, but with type G appearing occasionally. The only other large genus is *Gazania*, in which the numerous, narrow setæ of type F are sometimes difficult to distinguish from the hairs of the cypsela. The

tendency to reduction towards type N which appears rarely in the Arctotidinæ is more developed in this sub-tribe, appearing in three genera.

The Gundeliinæ is a small group with the pappus of type F, connate at the base, or the reduced form, type N.

Anthemideæ. The pappus here is usually reduced to the fimbriato-coroniform type when present, but in a large proportion of the genera it is entirely absent. In a few genera, such as *Athanasia*, *Lepidostephium*, *Allardia*, *Isoetopsis*, and *Marasmodes*, the evolution of type N has proceeded only as far as type F, the paleaceous setæ being connate at the base and quite short in several of the above genera. The next step is seen in other genera, such as *Anacyclus*, *Anthemis*, *Pentzia* and *Crossostephium*, where the pappus in some species is very short and the fimbriato-coroniform type is more common. In many of these genera and others of the tribe type Qb occurs, e.g., some species of *Chrysanthemum*, *Cotula*, *Pentzia* and *Anthemis*; or the pappus may be type N, or type Qb, or absent in different species of the same genus.

Interesting transition forms occur in the various species of the anomalous genus, *Oedera*, types N and F occur in addition to a special form somewhat like type K but with the paleæ fused by their margins to give a deep, membranous tube, fimbriate at the top.

In only one genus, *Cancrina*, are the paleæ few in number, type M, and in some species of the most closely allied genus, *Allardia*, setæ more or less flattened, but closely approximating the typical pappus of the Senecioneæ, occur. Other species of *Allardia* show these setæ developed into type F, with the length reduced and the setæ connate at the base; the apex of the setæ may be simple or plumose. In *Allardia* and *Cancrina*, therefore, we get a complete series of transition forms leading from type A to types N and M.

As *Oedera* and *Allardia* are in separate sub-tribes we again get no indication of the relative position of the Anthemidinæ and Chrysanthemidinæ and it becomes probable that the Anthemideæ, like the Cichorieæ, is sub-divided on an artificial basis.

Inuleæ. The Gnaphaliinæ is taken as the primitive sub-tribe and the Helichryseæ as the primitive group within that sub-tribe, the Eu-gnaphalieæ being derived. This arrangement is confirmed by the structure of the pappus. *Helichrysum* and *Gnaphalium* are the chief genera; the former has one row, or rarely several rows,

of setæ of type A, or occasionally the setæ are barbellate or sub-plumose at the apex, and may be free or connate in various ways at the base. The latter is similar, but the setæ are never in more than one row and sometimes have the cilia of the plumose apex fused, giving thickened and club-like setæ. Here also the setæ are free or connate at the base. The other genera are mostly setose and similar to the above, connation at the base being common and leading to the paleaceous and fimbriato-coroniform types in a few genera of the Helichryseæ.

The barbellate and sub-plumose types of the primitive genera, develop in others into types plumose at the base, as in *Helipterum*, or at the apex, as in *Podotrocha*, or the setæ may be scabrid, barbellate or plumose, as in *Waitzia*. Types A, D, E, F, G, M and N occur in this sub-tribe, the primitive types A and D predominating.

Types A and D are characteristic of the Tarchonantheæ (cp. Fig. 7, Chap. II). The higher types L and K occur in several of the Filaginæ, but this sub-tribe also shows types A and D in two of the chief genera, *Filago* and *Ifloga*, and type N in two smaller genera. The pappus may be absent occasionally in most genera and is never present in several.

Types A and D are again common in the Plucheinæ (cp. Fig. 7), but type E occurs in *Pterigeron* and F in two small genera. The relatively higher type D is commoner in the Inulinæ than in the lower groups (cp. Fig. 7), as are also types E, F and K, while in a few isolated genera the number of paleæ becomes reduced. The pappus may be in one to several rows and is frequently in two, the inner setose and the outer paleaceous.

The Angiantheæ, Relhaniinæ and Athrixiinæ show a very similar range, varying even in the same genus from type A to types K or M, and showing in general the types on the evolutionary lines leading to types I and M (see Fig. 18).

The Bupthalmiæ are of special interest as an intermediate group (cp. Fig. 7). Most of the genera have only one or two species and setæ of type A occur only in *Gymnarrhena*. Similar setæ but with the apex barbellato-plumose occur in *Rhanterium*. In the other genera the pappus is either absent or paleaceous of various types. Even in *Gymnarrhena* there is an external row of eight to ten setæ of type F, and in *Rhanterium* the setæ are reduced to four or five. The paleæ in the other genera are usually numerous and short, sometimes fused to give type N, sometimes prolonged into aristæ, as in type G.

Cynareæ. The Centaureinæ is taken as the primitive sub-tribe and in the chief genus, *Centaurea*, we find a wide range of pappus-forms; the setæ are in numerous rows and show various stages in fusion from the inner setæ of type A to the outer short paleæ of type K; types A, C, D, E, F, H, K, L and M occur, some of them in the same species, some of them in different species of this diversified genus. This covers the range in the other genera but these show a more limited variety of pappus forms. The plumoso-setose type is frequent in the Carduinæ but types A, B, C, D and F occur and are frequently connate at the base, a condition which is not common in the Centaureinæ. *Gymnarrhena* is, therefore, a very good intermediate form, leading on to *Centaurea* on one hand and by a similar development of paleaceous setæ to the rest of the Bupthalthinæ on the other.

The Plucheinæ were suggested as an alternative source for the Cynareæ (Chap. IV, F), but the pappus of the chief genera in that sub-tribe is of type A, so that it seems more probable that the Centaureinæ, at least, have come from the Bupthalthinæ. Polyphyly is, of course, possible and the Plucheinæ would form a probable source of the Carduinæ.

Type E is strongly developed in the Carlininæ but paleaceous types also occur and show a tendency to reduction, *e.g.*, in *Xeranthemum*, where the pappus may be absent or composed of minute paleæ. This leads on to the Echinopsidinæ where the pappus is of types F or N.

Mutisieæ. Here the Nassauviinæ are the primitive sub-tribe. The corolla form of *Nassauvia* (see Fig. 10, Chap. IV), suggests that genus as primitive but the pappus is frequently more or less paleaceous and the genus has a very peculiar habit. *Perezia* and *Trixis* are two of the chief genera and have the pappus of type A; of these two genera, *Perezia* has a very distinct habit and involucre, while *Trixis* closely approaches *Senecio* in several of its plant forms and in its involucre. It will be noted that the hairs on the cypselæ are also very similar (see above Sect. A), and that the style is the same as that of *Senecio*. It only requires a development of basal appendages to the anthers (these appendages are already present in a number of species of *Senecio*) and the development of bilabiate florets throughout the capitulum (which it has been suggested is the effect of excessive nutrition, Chap. IV, C) to change a *Senecio* into a *Trixis*. The mutations necessary for some, at least, of the generic differences in the Compositæ will be seen from this to be

quite small, (cp. the origin of the Cichorieæ from the Senecioneæ, Chap. IV, B).

In the other genera of the Nassauviinæ types D and E are common; type F and a type between E and M occur in *Nassauvia*, and the number of paleæ may be reduced in that genus and is usually so in *Triptilion*. Types E, F and G occur in the Barnadesiinæ and types A-F in the Onoseridinæ. In connection with the suggestion of *Mutisia* as the primitive genus in the latter sub-tribe (see Chap. IV, F), it is interesting to note that the pappus there is the same as the dominant form in the Nassauviinæ, i.e., type E.

The Gerberinæ are suggested to have come from *Mutisia* but type A is the commonest pappus-form in this sub-tribe, while *Mutisia* shows only type F. An allied genus, *Onoseris*, has type A pappus and on this point seems a more probable source. Types D and E also occur in the Gerberinæ. The plumoso-setose type is dominant in the Gochnatiinæ but types A, C, D, K and M occur in a few species. The appearance of the paleaceous types confirms the position of this sub-tribe, but the evidence of all the characters of the florets supports the conclusion that *Mutisia* gave the Gochnatiinæ and *Onoseris* the Gerberinæ.

Vernoniæ. The chief genus in this tribe is *Vernonia*, and the other genera are really more or less sub-genera of this large one. Most of the floral characters point to *Vernonia* being the primitive genus of the tribe and this is also borne out by the pappus. There are usually two, sometimes three, rows of setæ, which are frequently all type A and numerous; the inner row is usually of type A but occasionally of types F or K, and may be free or connate at the base; the outer row is usually of an abbreviated type K but quite frequently is setose scabrid (type A). A reduced number of setæ is present in some species especially in the African and Asiatic sections, or the pappus may be altogether absent. If this range of variation be compared with that of *Senecio* and more closely with that of *Liabum* (see above) the derivation of *Vernonia* from *Senecio* via *Liabum* is seen to involve only a few changes in the characters of the florets.

Type A is commonest in the rest of the Vernoniinæ; in a few genera types N, F and K occur and the pappus is occasionally absent.

Paleaceous types are dominant in the Lychnophorinæ, while two of the chief genera frequently show type A but types F and K also

occur in these genera, and the fimbriato-coroniform type is shown by other smaller genera.

Astereæ. The Homochrominæ is taken as the primitive sub-tribe; type A is dominant with type D as a common variation and types F and O in a few genera. In the small genus, *Homochroma*, the setæ are plumose, type E. There is also a tendency to abbreviation and connation of the setæ. This same tendency is more strongly developed in the Bellidinæ, leading in most genera to type N or to complete reduction. In the chief genus, *Brachycome*, abbreviated forms of types A and F occur and are sometimes connate, so that it is probable that the Bellidinæ have arisen from the Homochrominæ.

Type A is again dominant in the Conyzinæ and Baccharidinæ, with a tendency to connation at the base in a few genera and the same approach to type F, and more rarely to type E, as occurs in the Homochrominæ.

The five chief genera of the Heterochrominæ are *Aster*, *Erigeron*, *Olearia*, *Felicia* and *Celmisia* and these all show type A. There is, however, a large number of smaller genera in which types D, F or O occur. Types E, N and M occur more rarely. The advanced position of the Heterochrominæ compared with that of the Homochrominæ, which was suggested by the colour of the corolla (Chap. IV, D), is confirmed by the greater development of the types E, F and O in the former sub-tribe.

The pappus is frequently absent in the small sub-tribe, Grangeinæ, and when present is usually of the reduced type N, or an abbreviated form of the fimbriato-paleaceous type K, which is very closely allied to type N.

Eupatorieæ. The primitive sub-tribe here is the Ageratinæ and within the sub-tribe the *Eupatorium-Mikania* group is basal. In these two genera type A is the usual pappus-form; the setæ are frequently connate at the base and type D also occurs rarely. There is a marked tendency to fusion of the setæ, and types E, F, G, K and O all occur. Reduction is sometimes present giving type N, or no pappus at all, or the number of aristæ or paleæ, which varies from many to two, may be reduced to five, ten or twelve. This reduced number of members may or may not be associated with the vascular bundles of the pericarp but when ten or five are usually so associated.

This tendency to reduction shows clearly in *Sclerolepis*, a transition genus between the Ageratinæ and Piqueriinæ (see 61b.

Figs. 3-5), and is continued in the latter sub-tribe, giving 3-5 aristæ in *Adenostemma* and type N in *Piqueria*. Type E which is common in the Ageratinæ also occurs here in three genera and types G and K in other genera. Type A is again dominant in the Adenostylinæ with types D and B as common variations. All three types occur in *Brickellia*, the chief genus, and type G occurs also but only in *Carphochaete*.

Heliantheæ. The aristate type O and its derivatives (see Fig. 18) form the dominant types in this tribe. The tendencies to lateral fusion and reduction giving the paleaceous and fimbriato-coroniform types are also present, but to a smaller extent.

The Verbesininæ is taken as the primitive sub-tribe and frequently shows only two aristæ; that this is a reduced not a primitive pappus-form will be clear from the above account of the pappus (Sect. B) and this view is supported by the fact that the other reduced form, type N, is also of frequent occurrence in this same sub-tribe, and also by the fact that the pappus is frequently absent altogether. The setose origin is further demonstrated by the frequent presence of paleæ of types K and L (which are clearly fused setæ) between or among the aristæ, and by the *Helianthus* type, which is type N, with two of the major lacerations larger than the others, thus passing locally into type K.

The pappus is absent from the Ambrosiinaæ, except in one genus, *Dicoria*, which shows a feebly developed type N structure. In the Petrobiinaæ the pappus is absent or of type N in combination with 2-4 structures of type G. This same combined type, where a few of the fimbriations of type N become thickened and elongated, thus passing locally into type G, occurs in the Lagasceinaæ.

The Zinninaæ usually have the pappus absent, but type O is present occasionally. The Coreopsidinaæ are characterised by type O frequently developing into types Pa and Pb or being reduced to types R or Qa. The pappus is also sometimes absent, so that the tendency to reduction reaches its extreme expression.

This tendency to reduction is developed further in the Melampodiinaæ, the pappus here being frequently absent, and showing only types R, Qa and N when present, except in a few cases where types O and G occur.

The tendency to reduction is even more accentuated in the Milleriinaæ (cp. Fig. 7), where in most genera the pappus is entirely absent, showing type N in only two genera and four aristæ of type O in another genus.

The affinity between the Galinsoginaæ and Madiinaæ which is

suggested in Fig. 7 is emphasised by the pappus characters. In the Galinsoginæ the tendency to lateral fusion shown in the Verbesiniæ is further developed, the pappus being usually of types G or M. The Madiinæ have more in common with the Coreopsidinæ in that type N is dominant, but type G occurs in *Wilkesia*, and occasionally in *Layia*, which genus also shows type E, which it will be remembered gives type M (see Figs. 17-18). Type K also occurs occasionally in *Achyrachæna*.

Heleniæ. The tendency to lateral fusion of the setæ which shows in the Galinsoginæ becomes dominant in the Heleniæ. Types A and D occur within this tribe only in the Tagetinæ, which is taken as the primitive sub-tribe, but as these types are practically absent from the Heliantheæ their presence in several of the Tagetinæ raises the question of the origin of that sub-tribe.

There are several possible explanations; the most probable one is that the reclassification of this tribe is required. The Heleniæ, like some of the other tribes, is not a very natural group; indeed, Bentham put forward this tribe with some uncertainty (cp. 5, p. 381). It is distinguished from some of the Heliantheæ only by the absence of paleæ from the receptacle, and the genera with the pappus setose are practically Senecioneæ in all their characters, except the slight tendency of the setæ to be paleaceous at the base. This, it has been pointed out above occurs even in the genus *Senecio*, but Bentham seems to have been unaware of the fact.

Apart from these anomalous forms the Tagetinæ usually shows type G, but types K and L also occur. The Flaveriinæ are a small group with type G or the reduced type N or no pappus at all. The Heleniinæ are usually type G, but one genus, *Trichoptilium*, shows type L, and another, *Psathyrotes* (removed to the Senecioninæ by Hoffmann) shows B.

The Baeriinæ usually have the pappus of type G, but a considerable variety occurs which it is unnecessary to discuss in view of the contemplated reclassification of the tribe. The chief point to note is the appearance of type N in a number of genera and the complete absence of the pappus in a number of others. This leads on to the stronger development of type N in the Jaumeinæ, cp. Fig. 7.

D. PHYLOGENETIC SIGNIFICANCE OF THE PAPPUS.

The spasmodic variation of the pappus in related genera has been pointed out in Section A, but the pappus-forms when treated on broad lines as in Section C are capable of yielding valuable

phyletic data, provided that critical tendencies are considered to be of as much importance as actual form. Two such tendencies, *i.e.*, cohesion and reduction which are fundamental tendencies in the other parts of the floret, can be recognised as being ruling factors in the development of the paleaceous, aristate and coroniform types from the primitive setose types. These lines of orthogenesis are the key to the otherwise hopelessly confused mass of variations shown by the pappus.

Many of the points where the pappus-form has a phyletic value have been indicated in Section C so that it is only necessary to summarise briefly the phyletic value of this part of the floret.

Senecio is confirmed as the basal genus, by the dominance of the most primitive pappus-forms and the occasional expression of the two fundamental tendencies above-mentioned. The basal position of the *Senecioninæ* is also confirmed by the same facts and the lines of evolution leading to the higher types of pappus are traced in outlying genera.

The *Liabinæ* are confirmed as an intermediate stage in the development of the *Vernoniæ* and the derivative position of the *Lychnophorinæ* is also verified.

The origin of the *Cichoriæ* from the *Senecioninæ* is confirmed and the progressive development of the two critical tendencies together with the frequent presence of the primitive types is clearly shown.

There is also evidence in support of the suggested origin of the *Calendulæ* as a reduction product of the *Senecioninæ*.

The evolution of type M from type E occurs in the origin of the *Arctotideæ*, *Ursinia* again being the basal genus, with the *Gorteriinæ* as a progressive variation and the *Gundeliinæ* as a reduced derivative.

In the *Anthemideæ* the tendency to reduction is more strongly developed, leading to the frequent absence of the pappus or its presence in the form of type N. The occurrence of transitions from type A through F to N is evidence in support of the suggested origin of this tribe from the *Senecioninæ*.

The *Inuleæ* show a very marked progressive evolution in the pappus forms from the *Gnaphaliinæ* (type A usually) to the *Inulinæ* (types A, D, E, F and K), with type A passing into types D, E, F and G in the *Buphthalminæ* leading to the *Cynareæ*, where the higher setose and paleaceous types are well developed.

In the *Cynareæ* *Centaurea* is confirmed as the primitive genus, with the positions of the *Carduinæ*, *Carlininæ* and *Echinopsidinæ*

as in Fig. 7. The possible polyphyletic origin of the Cynareæ is suggested and the Plucheinæ are indicated as a possible alternative source of the Carduinæ.

The most interesting point is the confirmation of the origin of the Nassauviinæ from the Senecioninæ and the primitive position of that sub-tribe in the Mutisieæ. *Trixis* is clearly the primitive genus; this is confirmed by the character of the achenial hairs. *Mutisia* is confirmed as the primitive genus in the Onoseridinæ, with *Onoseris* as a closely allied basal genus giving the Gerberinæ, while *Mutisia* is the source of the rest of the Onoseridinæ and of the Gochnatiinæ.

The rearrangement of the Homochrominæ (Astereæ) below the Heterochrominæ is confirmed. The positions of the other sub-tribes are also supported by the evidence derived from the pappus with the exception of the Bellidinæ, which it is suggested were derived from the Homochrominæ, not independently as in Fig. 7

The origin of the Eupatorieæ from the Astereæ by the passage of the Heterochrominæ into the Ageratinæ and the position of the *Eupatorium-Mikania* plexus at the base of the latter sub-tribe are upheld by the present evidence, as is also the passage of the Ageratinæ into the Piqueriinæ via *Sclerolepis*, *Adenostemma*, and *Piqueria*.

The Heliantheæ again show advanced characters, the tendency to fusion in clumps and reduction being well-developed in the primitive sub-tribes, while the tendency to lateral fusion of the setæ culminates in the paleaceous forms of the Galinsoginæ.

The possibility of the Helenieæ being an artificial group is indicated and a close affinity of many of the genera with the Senecioninæ is traced, while the evolution of the sub-tribes is left for future consideration on account of the variation in the form of the pappus.

It is clear, therefore, that the consideration of the pappus in the light of the evolution of the various types from the primitive setose form confirms the previous phyletic suggestions in most of the more important points, and even furnishes valuable indications of the more detailed evolution of certain groups such as the Vernoniæ, Eupatorieæ, Cynareæ and Mutisieæ.

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CHAPTER VI.

THE INVOLUCRE.

THE characters of the involucre have been used more or less empirically in various systems of classification, but there appears to have been no critical consideration of the origin and homologies of this structure.

As the involucre is present fully developed in practically all Compositæ it is necessary to consider the evolution of involucreal structures in other families where its origin and development can be traced. This is done in Section B of the present chapter which in addition contains a brief account of the history of our knowledge of the involucre in the Compositæ, an analysis of the various types to be found in the family and an indication of the bearing of that variation on the previous phyletic conclusions.

A. HISTORY.

As the involucreal bracts are easily observed and show a great variety of form they received a considerable share of the attention of the earlier systematists. Vaillantus (II, 70¹) used the involucre for his primary divisions of the Cynarocephalæ; Magnol (I, 62) who used the "calyx" as his basis for classification, characterises his "Compositum" as "calice externo includente florem"; Boerhaave (I, 12) gives the involucreal characters for each genus; Linné (I, 59) gave a "methodus a calycis" of his own, dividing the "Communes" into eight groups on the character of the involucre. He distinguished various types of involucre such as simple, uniseriate, duplex, calyculate, involucreate, multiseriate with all the bracts similar or imbricate. Berkhey at a later date (I, 9) gave figures of various types of involucreal bracts and considered the involucre in some detail, distinguishing the simple, imbricate and calyculate types.

The involucre was used with other parts by Don (I, 25) in his classification of the Cichoriæ, and Gærtner (I, 32), although he did not use this structure for his larger groups, described it carefully for each genus. The involucre is now included in the

¹ Roman numerals refer to previous bibliographies.

essential characters of all genera, and is also used in the classification of species within various genera, such as *Pteronia* (9), *Centaurea* and *Liabum*.

Cassini (I, 18, Tome I, pp. 255-260) distinguished between the inner involuclral bracts, which are usually more or less membranous, and the outer involuclral bracts, which may be very small and rather irregularly arranged or large and closely similar to cauline leaves. He named the collection of inner bracts the "péricline," and the outer bracts when foliaceous the "involucre." Where the outer bracts are small this author considered that a "péricline," accompanied by bracteoles is present. In addition he described the variation in the form of the pericline and involucre at some length, giving the technical terms used in describing the appendages, margins, etc.

Bentham (I, 7) considered this distinction of pericline and involucre to be misleading, and adopted the general term "involucre." This practice has been followed very generally, the difficulty of the cases with foliaceous outer bracts which pass more or less gradually into cauline leaves being met by describing the involucre as duplex. Bentham also discussed the taxonomic value of the involucre, pointing out that this structure may give useful indications of tribal affinities, but must be used with caution on account of its variability even in related genera.

Morphology. Cassini (*loc. cit.*) considered that the members of the pericline were the rudiments of petioles with flowers developed in the axils of all, if uniseriate, or with flowers aborted in the axils of the outer rows, if multiseriate. The members of the "involucre" he homologised with cauline leaves. The leaf base nature of the periclinal bracts is confirmed by Church (3). Bentham (*op. cit.* p. 367) apparently considered all the involuclral members homologous with the flower-bearing, inner bracts. The bract-like nature of these inner members is confirmed by various abnormalities, such as that recorded by Offner (IV, 65 and see also descriptions of proliferations by Masters, IV, 52, and Worsdell, IV, 97), and by Church's observations (see Chap. VIII, B). The spines of the anomalous genus, *Xanthium*, were described by Baillon (V, 3) as involuclral bracts.

The morphology of the outer involuclral members has never been seriously considered, with the exception of Cassini's few remarks, which have been neglected by most synantherologists. Blake (2) and others, however, have noted the similarity of these so-called bracts to reduced cauline leaves.

Biology. The occasional use of the involucre in the wind-dispersal of the whole fruit-head was noted by Hildebrand (V, 30). The protective function and the hygroscopic movements of the bracts are mentioned by Haberlandt (III, 15, p. 552) and Yapp (IV, 98), and form the subjects of short papers by Rathay (12) and Gressner (6). The latter also mentions the hairs which seal the closed involucre in the bud. These had been noted previously by Hildebrand (*loc. cit.*).

Biometrics. As the result of extensive statistical observations Shull (13-14) concluded that the number of involucre bracts shows a seasonal variation due to nutrition differences. The number showed a continuous change, beginning low, increasing for 2-6 days to a maximum and then decreasing for the rest of the flowering period. Shull maintains that the modes of his curves have no connection with the Fibonacci series.

Harris (7) deals with the correlation between the number of involucre bracts and the number of fruits developed.

Mutations. Sudden variations in the involucre are recorded in a few cases, *e.g.*, partial loss of prickles in *Xanthium Woottoni* (IV, 87, pp. 139 and 152), and a peculiar spreading and variation in number of the bracts in *Vernonia rubricaulis* (15). Various abnormalities, chiefly apostasis, are mentioned by Cramer (IV 21) and Masters (IV, 52).

B. ORIGIN AND DEVELOPMENT OF THE INVOLUCRE.

The capitulum is a racemose inflorescence, usually with a more, or less flattened receptacle on which the florets are crowded. It is frequently considered to be a spike of sessile or nearly sessile flowers with the peduncle shortened. There is, however, another possibility which is usually overlooked—the capitulum may arise by the abortion of the pedicels in a racemose umbel. The two processes are very similar, but in the former the pedicels abort first and then the peduncle, while in the latter the stages are reversed. Although the reduction is similar the products would tend to present certain differences.

In a spike the flowers are usually spaced well apart and the flowers are frequently large. Any reduction in the length of the peduncle would naturally be gradual, and the bracts of the flowers would tend to be reduced by the same causes (decrease in food supply, illumination, etc.), and, therefore, in the same measure as the flowers. The receptacle would rarely, if ever, become flat, and

would tend to be conical and elongated with the subtending bracts of the flowers reduced but still present (cp. Fig. 19, A-B).

In a racemose umbel the flowers are usually already crowded together. The food supply is already reduced, so that the flowers are small, and, as the outer flowers receive more illumination, they tend to become zygomorphic (cp. Goebel, V, 21, p. 552). The pedicels at their insertion on the peduncle are much more crowded than the florets at the top of the umbel, so that the bracts of all except the outer flowers have already become reduced or have disappeared completely. If abortion of the pedicels occurred the florets would then be sessile on a more or less flat receptacle with very reduced bracts to the inner florets or no inner bracts at all. The bracts of the outer florets would form a structure corresponding to the pericline of Cassini (cp. Fig. 19, C-D).

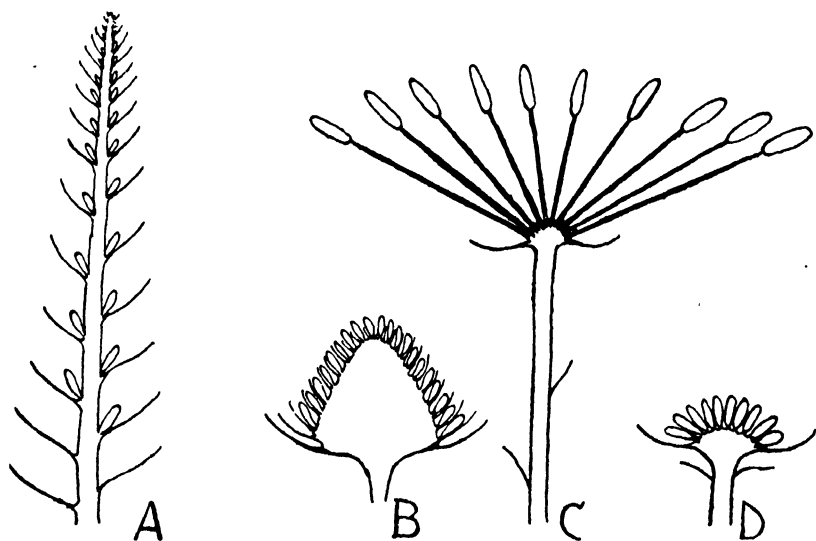


FIG. 19. *Origin of the Capitulum.* A—spike; B—capitulum derived from spike; C—racemose umbel; D—capitulum derived from racemose umbel.

Parkin (10), although he does not discuss the evolution of the involucre at all and makes only a passing reference to the origin of the capitulum, gives a diagram (op. cit. Pl. 18) in which the spike is regarded as a side line and the head as derived from the simple raceme via the corymb and the *umbel*. Masters (IV, 52) records anomalous elongation of the pedicels in *Hypochaeris radicata* and *Senecio vulgaris*, etc., by which change "the capitulum assumes the appearance of a simple umbel."

The involucre inflorescence occurs as a normal form in quite a number of families, e.g., Dipsacæ, Umbelliferæ, Cornacæ, Proteacæ and Eriocaulacæ, and in many others as an exceptional

type, e.g., *Sphærocoma* in the Caryophyllaceæ (cp. 1, Tab. III), where the involucral bracts are few, small and green; *Posoqueria densiflora* (Rubiaceæ) where there is practically no receptacle and an indefinite involucre of a few foliage leaves; and *Monarda* in the Labiatæ (see below).

It may be of interest to note the condition of the involucre in some of these families. In the Monocotyledons *Alisma* *Plantago* shows cymose umbels with a simple involucre very similar to that of the proliferated *Helenium* observed by Masters (II, 48); *Narthecium ossifragum* may be taken as an example of the common phenomenon of progressive crowding in a raceme with bracts and pedicels present, spacing taking place later in the fruiting stage. In the crowded spikes of many orchids bracts are usually present.

Among the Dicotyledons we have the phenomenon of progressive crowding very marked in the Cruciferæ, where the bracts are absent; this with the corymbose habit gives an approach to the racemose umbel. In the Leguminosæ dense racemes are common; the pedicels are frequently very short and the bracts much reduced or absent. An involucre is comparatively common in these heads, and may be composed of a few of the outer fertile bracts or 1-2 slightly modified cauline leaves.

In the Araliaceæ (*Hedera* and *Aralia*), the inflorescence is a racemose umbel with the bracts much reduced or absent and no involucre. The Umbelliferæ frequently show the umbel with only the outer bracts forming a uniseriate involucre, but the development of more rows of involucral bracts occurs whenever the inflorescence becomes denser, as in *Sanicula*, where it is uniseriate or indefinitely bi-seriate, and *Astrantia*, where it is bi- or tri-seriate.

The cauline origin of the involucre in *Monarda* is seen clearly in the Labiatæ, where there is a distinct tendency towards shortening of the internodes immediately below the inflorescence. This is well shown in many common Labiatæ, such as *Prunella vulgaris* and *Ajuga reptans*, and a similar phenomenon is seen in *Campanula glomerata*.

✓ In the Campanulaceæ the umbel of *Fasione*, like that of *Astrantia*, has a pluriseriate involucre. The usual tendency in the Lobelioideæ is towards dense spikes with many large foliaceous bracts, but racemose umbels occur also, notably in *Siphocampylus* spp. Below these umbels there are usually a few normal foliage leaves, somewhat crowded on account of the shortening of the internodes as in the Labiatæ.

These few examples serve to illustrate the two sources of the involucre in other families. In the one case the involucral members are the bracts of the outer florets, *e.g.*, Umbelliferæ and some Leguminosæ; in the other case the involucre is composed of purely cauline leaves, *e.g.*, some Leguminosæ, *Anemone*, *Nigella* and *Siphocampylus* spp. The tendency to form secondary aggregations of capitula is present in several families in addition to the Compositæ, and may be illustrated by *Xylia Kerrii* in the Leguminosæ (4).

As the pluriseriate involucre arises either by the progressive sterilisation of successive rows of bracts or by the progressive aggregation of cauline leaves the primitive involucre is obviously the type with a limited number of bracts arranged more or less in one row as in the Umbelliferæ, with or without a small and indefinite number of reduced cauline leaves.

The difference in origin corresponds very closely with Cassini's "péricline" and "involucre"; and the uniseriate pericline is clearly the primitive type with no sterilisation of bracts, while the "involucre" of a few more or less scattered members is likewise in the primitive condition.

The term "pericline" will be used here to indicate the leaf-base structures of the involucre which have, or which probably have had, florets in their axils. As the term "calyculus" is in common use it will be used here to denote the outer part of the involucre which originates from purely cauline leaves. This obviates the difficulty of the variation in terminology, duplex involucre, secondary involucre, pseudo-involucre, etc., having been used in various attempts to distinguish between the two parts of the complete involucre (cp. Blake, 2).

Cassini's distinction between reduced and foliaceous members of the calyculus does not seem to be of much importance, when the mobile condition of the vegetative parts, especially in a dense inflorescence, is recognised. The homology of these reduced cauline leaves is obvious in such cases as *Cavea* (IV, 78, Pl. V) where reduction proceeds simultaneously with the progressive aggregation of the cauline leaves, and also in *Gynura elliptica* (8, Pl. 11), *Senecio crepidiformis* and *S. Pearsonii* (11, Figs. 8-9). The not infrequent occurrence of apostasis in the calyculus is due to the elongation of nodes which are normally suppressed.

As the complete involucre of the Compositæ usually includes both calyculus and pericline it seems that both cauline leaves and floral bracts contribute to this part of the capitulum.

The only point now to be determined is whether the capitulum arose from a spike or from a racemose umbel. The smallness and flatness of the receptacle, the very reduced character of the receptacular bracts when they are present, the small size of the individual florets and the dominant tendency to zygomorphy of the outer florets are all evidence in favour of the origin of the capitulum by the suppression of the pedicels in a racemose umbel.

The only evidence in favour of the origin from a spike is the occurrence of an elongated receptacle together with receptacular bracts in a few of the *Helianthæ*, such as *Rudbeckia*, but these are quite advanced in the characters of the style, stamens, corolla and pappus, so that they can scarcely be considered primitive types. This derivation would also leave unexplained the small size of the florets, the dominant tendency to zygomorphy in the outer florets, the reduced condition and frequent absence of the receptacular bracts and, more important still, the dominance of the small, flat or very slightly convex receptacle. All these characters and tendencies are more readily intelligible when the racemose umbel is taken as the ancestral inflorescence.

The view adopted here of the origin and development of the involucre in the *Compositæ* is briefly as follows: The ancestral racemose umbel by abortion of the pedicels gave a capitulum with the bracts of the outer florets forming a uniseriate pericline, while aggregation of the cauline leaves immediately below the inflorescence gave the calyculus. The primitive involucre has, therefore, an uniseriate pericline with a calyculus composed of a few scattered members. Progressive sterilisation of the floral bracts has given the pluriseriate pericline, while progressive aggregation of the cauline leaves has given a denser, pluriseriate calyculus.

It must be observed, however, that in some cases the calyculus passes gradually into the pericline, but that is a question of phyllotaxis and is considered in Chapter VIII.

C. ANALYSIS OF THE INVOLUCRE IN COMPOSITÆ.

Taking the uniseriate pericline and the slightly developed calyculus as primitive we can now analyse the distribution of the various types of involucre in the family.

Senecioneæ. The genus *Senecio* again shows the primitive type with a number of variations. The pericline is uniseriate with the bracts free or more or less connate at the base, or there may be a smaller number of "bracts" in a second row. These outer "bracts" are probably a development of the smaller leaves of the

calyculus, which is frequently present. The members of the calyculus may be few and very small, as in *Senecio vulgaris*, *S. Doria*, etc., but even in these species the number is sometimes as many as eight; or the calyculus may be multiseriate with the inner members almost equalling the periclinal bracts as in *S. paniculatus*; or there may be no calyculus. A multiseriate calyculus of 20-40 leaves occurs in *S. lavandulæfolius*: other similar cases are the species of the section *Leptolobi* of Harvey and Sonders,

The involucre in most of the genera of the Senecioninæ is similarly uniseriate, with or without a calyculus; even in this sub-tribe, however, the involucre rapidly becomes biseriate, as in *Arnica* spp. and *Doronicum*, or triseriate as in *Bartlettia*, or multiseriate as in *Melaleuca* and *Culcitium*, or as in *Eriothrix* the involucral bracts may be almost indistinguishable from the densely crowded, reduced leaves of the stem. *Culcitium* is an interesting genus, as it differs from *Senecio* only in the multiseriate involucre, which on a larger scale closely resembles that of *S. paniculatus* in the gradual diminution in the size of the outer involucral members. As is usually the case where an artificial distinction is made, the two genera *Senecio* and *Culcitium* pass into each other by intermediate species which have been placed sometimes in one genus and sometimes in the other. Indeed, a new genus, *Shafera*, has been founded (5) which differs only in the 3-4-seriate involucre and obtuse style branches, and which is regarded by its author as intermediate between *Senecio* and *Culcitium*. It seems probable, therefore, that the multiseriate involucre in the Senecioninæ is due to a development of the calyculus, the pericline remaining uniseriate.

The Tussilagininæ are usually uniseriate and the Liabinæ multiseriate; the Othonninæ are uniseriate and are characterised by the greater development of the tendency to connation which is present in *Senecio*.

Cichorieæ. The involucre in this tribe is very varied; frequently the pericline is uniseriate, with a well developed, more or less foliaceous calyculus in one to many rows. The progressive aggregation of the cauline leaves to form the calyculus is occasionally seen in the dandelion. The sub-tribes are again indistinguishable on this character, but the structure of the involucre is closely allied to that of the Senecioninæ.

Calenduleæ. Here the involucre is usually uniseriate with or without a calyculus but is sometimes triseriate in *Osteospermum*, where the calyculus may equal or may be smaller than the pericline.

Arctotideæ. The involucre is multiseriate in all genera except *Landtia* where there are only a few rows of bracts. The calyculus is in a more or less primitive condition in the Arctotidinæ and more developed in the other two sub-tribes.

Anthemideæ. The calyculus is distinct in a number of genera and the pericline uniseriate or biseriate. The number of rows in both pericline and calyculus varies considerably but more or less similarly in the two sub-tribes.

Inuleæ. In the Gnaphaliinæ the Helichryseæ show a larger proportion of genera with the involucre in the primitive condition, i.e., pericline uniseriate, calyculus in one to a few rows. In some genera, such as *Millotia* and *Quinetia*, the involucre closely resembles that of *Senecio*.

A similar condition obtains in the Tarchonanthinæ, one genus having the primitive form and the others a more developed calyculus. In the Filagininae most genera have only a few bracts, only *Filago* and *Cylindrocline* showing sometimes the multiseriate involucre. The range in the Plucheinae from a pauciseriate to a multiseriate involucre is covered by *Pluchea*, except the case of *Denekia*, which has a uniseriate pericline and a few similar outer leaves forming the calyculus.

The Athrixiinae are all multiseriate, while the Relhaniinae show a large proportion of the genera with the primitive involucre, *Bryomorpha* being similar to *Eriothrix* in that the involucre is practically indistinguishable from the reduced, densely crowded, cauline leaves. A number of the Relhaniinae have the multiseriate involucre while the Angianthinæ have only two genera, *Cephalopterum* and *Gnaphalodes*, with the advanced type; all the other genera have either the primitive type or a few, sometimes only two, bracts.

This fact and the difference in the corolla (see Chap. IV) suggests that the Angianthinæ are not so closely related to the other two sub-tribes as is suggested in Fig. 7. They might be better regarded as a special group showing a certain amount of reduction in the involucre, while the Relhaniinae might be regarded as giving the slightly more advanced Athrixiinae.

The primitive involucre occurs in a number of the Inulinæ and Buphthalminæ, and the numerous outer rows in the other genera are shown to be a developed calyculus by their frequently foliaceous structure. Indeed, the Inulinæ are as primitive as the Gnaphaliinæ in the involucre.

Cynareæ. The involucre is multiseriate and in the primitive

genus, *Centaurea*, has undergone various modifications; spines or more or less elaborate appendages are frequently present at the apices of the bracts. The pericline is in two or more rows, and usually passes gradually into the calyculus. A similar involucre without the elaborate appendages is the rule in the *Cynareæ*. The only difference in the sub-tribes is the occurrence of a more or less foliaceous calyculus in two or three genera of the *Centaureinæ*.

Mutisieæ. In the *Barnadesiinæ*, *Onoseridinæ* and *Gochnatiinæ* the involucre is multiseriate without exception. This is interesting when the involucre of the *Nassauviinæ* is considered; there only three small genera are multiseriate, the others varying from five or six bracts to a few rows. *Perezia* has two to many rows, the pericline being uniseriate and the calyculus frequently foliaceous. In *Trixis* the pericline is composed of from five to ten bracts in one row, and the calyculus is usually a few leaves, sometimes small, sometimes larger and foliaceous, rarely more numerous and in several rows. This is exactly the condition in *Senecio* (cp. Chap. V, Sect. D). In *Nassauvia*, where the cauline leaves are reduced and crowded they pass very gradually into the calyculus, cp. *Bryomorpha* and *Eriothrix*.

Vernoniææ. The involucre is multiseriate as a rule, reduced to a few bracts in *Corymbium*, *Rolandra* and *Spiracantha*, and pauciseriate in a few other genera. *Vernonia* and two or three other genera of the *Vernoniinæ* have the calyculus occasionally foliaceous.

Astereææ. The involucre is frequently multiseriate, but in the *Homochrominæ* an uniseriate pericline with a more or less foliaceous or reduced calyculus occurs in a number of genera and it is the rule in the *Bellidinæ* and *Grangeinæ*. This primitive involucre is the commonest form in the *Conyzinæ* and *Baccharidinæ*, but in both these tribes it is occasionally multiseriate. The *Heterochrominæ* is very similar to the *Homochrominæ* with even a larger proportion of genera showing the primitive involucre. The chief genera, however, are all multiseriate, except *Erigeron* and some species of *Felicia* which are biseriate.

Eupatorieææ. The involucre in *Eupatorieæ* varies from one to many rows, with the calyculus small or equalling the pericline in the size of the leaves. *Mikania* is distinguished from *Eupatorium* by its pericline of four bracts with or without a few membered calyculus. The other genera vary from uniseriate (*Stevia*) and bi- to triseriate (*Ageratum*) to pauciseriate (*Alomia*). The smaller genera vary within a similar range. In the *Piqueriinæ*, with the

exception of *Decachæta*, the primitive involucre is the rule. The multiseriate type occurs in the chief genera of the *Adenostylinæ*, a few others showing the primitive type.

Helianthææ. The primitive involucre is the rule throughout the *Helianthææ* with only a few exceptions. The difference between the pericline and the calyculus is frequently so marked that the involucre is known as duplex, even by those systematists who do not recognise the essential difference between the pericline and the calyculus which is commonly quite foliaceous in this tribe. There is so much similarity in the sub-tribes that it is unnecessary to consider them in detail with the exception of the *Madiinæ* where the calyculus is sometimes absent, and the *Galinsoginæ* where the uniseriate pericline and slightly developed calyculus confirm the affinity of that sub-tribe with the *Heleniææ*.

Heleniææ. Here the pericline is without exception uniseriate and the calyculus is absent or only slightly developed except in the more important genera of the *Jaumeinæ*.

D. PHYLOGENETIC SIGNIFICANCE OF THE INVOLUCRE.

The establishment of a sound view of the morphology of the involucre with a definite primitive type enables us, as with the pappus, to analyse with some clearness the large number of varieties of this part of the capitulum and to obtain some information of phyletic value.

The primitive position of the *Senecionææ* and *Senecio*, the passage of the *Senecioninæ* into the *Vernoniinæ* via the *Liabinæ*, the positions as in fig. 7 of the *Othonninæ*, *Tussilaginæ*, *Cichorieæ*, *Calenduleæ* and *Anthemideæ* are all confirmed. The *Arctotinæ* is clearly the primitive sub-tribe in the *Arctotideæ*.

A slight rearrangement of three of the sub-tribes in the *Inuleæ* is suggested and corroboration of the position of the others obtained. The *Centaureinæ* is confirmed as the primitive group of the *Cynareæ*. *Trixis* as the basal genus (arising from the *Senecionææ*) and the *Nassauviinæ* as the basal sub-tribe of the *Mutisiææ* have the involucre in the primitive condition.

The positions of the sub-tribes in the *Vernoniææ*, *Astereæ* and *Eupatoriææ* are confirmed.

The relative primitiveness of the *Helianthææ*, the derivation of the *Heleniææ* from the *Galinsoginæ* and the advanced position of the *Jaumeinæ* are supported by the evidence of the involucre.

Without exception, therefore, the characters of the involucre in the *Compositæ* substantiate the phyletic conclusions given in fig.

7, Chap. II and modified in Chaps. III-IV. This, it should be noted, is with the uniseriate pericline and slightly developed calyculus taken as the primitive type of involucre, a view which derives strong reciprocal support from the fact that with this hypothesis the involucre shows an evolution essentially similar to that of the other characters of the capitulum.

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CHAPTER VII.

THE RECEPTACLE.

WE have now reached a stage where it is admissible to use previous phyletic conclusions in the interpretation of the morphology and phyletic value of the remaining structures of the capitulum. As the structure and irritability of the styles and stamens, the structure and colour of the corolla, the structure of the pappus and involucre have all been shown to indicate the same evolutionary lines, the structure of the receptacle should be explained in the light of these facts. This is done in Section B and the usual sections on the history, the distribution of forms within the family and the phyletic value are included in the present chapter.

A. HISTORY.

Like the involucre, the receptacular paleæ are among the more obvious features of the capitulum and as such were used at an early date in the sub-division of the family. Vaillantus (II, 70) distinguished various sub-groups of the *Corymbiferae* and the *Cichoriaceae* on the basis of the naked, paleaceous or pilose nature of the "placenta." Pontedera (I, 71) distinguished naked, squamate, pappose, and villous types of "thalamus." Gaertner (I, 32) also used the receptacle for his sub-divisions, distinguishing the alveolate form in addition to previously recognised types. Berkhey (I, 9) has a chapter on the receptacle, distinguishing four types of surface and giving numerous figures in Tab. VII.

Cassini (I, 18, Tome I, p. 252) gives a very precise and detailed account of the variation in the receptacle or "clinanthe," distinguishing five parts and eight kinds of appendages, and differentiating between the paleæ with florets in their axils and paleæ which are more numerous than the florets and surround them. Bentham (I, 7, p. 368) gives another account of the variation in the receptacle and points out that the receptacular paleæ are homologous with the involucre bracts; Blake (2) also notes this homology. It applies, however, only to the members of the periclinal part of the involucre (cp. Chap. VI, B). Bentham apparently confused the two kinds of receptacular paleæ in the *Bupthalmineae* (I, 7, p. 369) but afterwards (I, 8, p. 337) noted the setiferous character in a number of

genera in that sub-tribe. He also (*loc. cit.*) criticises Don's use of the receptacle (I, 25) in the classification of the Cichorieæ.

Abnormalities. Cramer (IV, 21) refers to cases of the abnormal development of receptacular paleæ in *Hieracium* and *Pyrethrum*, in which there are normally no paleæ. Goebel (V, 21 p. 397) mentions gradual transitions from involucre bracts to setiform paleæ in *Xeranthemum macrophyllum*, but, as above-mentioned (Chap. V, A), he maintains that a qualitative change has taken place and that these "bristle-scales" are "bristle-scales" not paleæ.

Development. Kraus (V, 44) considered that the foveole was epidermal in origin, but Yapp (IV, 98) points out that although the ridge is epidermal, the floor of the foveole has a more deeply seated origin. The late appearance of the ridge of the foveole and its origin from the epidermis is also noted by Martin (II, 47).

Biology. The arching of the receptacle which occurs in *Taraxacum* and other genera, by means of which the stipitate, parachute pappus is accommodated on a more or less hemispherical surface, is noted by Benecke (1) and Kronfeld (3).

B. VARIATION IN THE RECEPTACLE.

Cassini's analysis of the various forms assumed by the receptacle and its appendages is more precise than Bentham's but the terms given by the latter will be used in the following description because they are in more general use.

The receptacle is usually flat or slightly convex, occasionally it is conical and more rarely it is concave. This dominance of the flat or nearly flat receptacle is explained by the suggested origin of the capitulum from a racemose umbel (Chap. VI, B), and it is worth noting that Bentham (I, 7, p. 368) regarded the elongated conical receptacle as a character of no more than specific value.

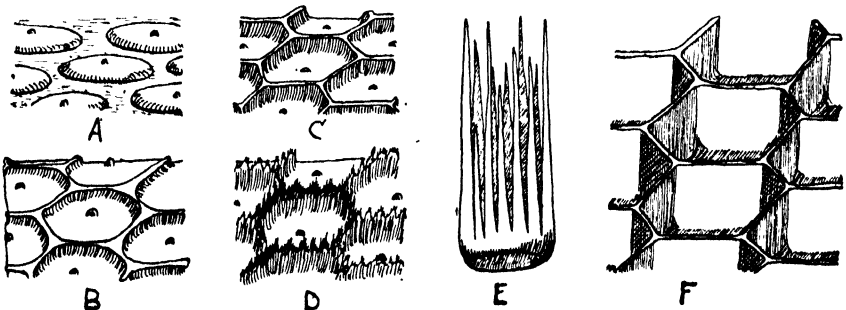


FIG. 20. *Receptacle Forms in the Compositæ.* A—scrobiculate; B—foveolate; C—areolate; D—flmbrillate; E—setiferous (one segment); F—alveolate, shallow alveoles with entire margins.

The surface of the receptacle is described as *scrobiculate* (Fig. 20, A) when it is covered with low mounds of tissue with furrows between, the top of each mound being occupied by the remains of the vascular bundle, which supplied the lower distributive centre (cp. II, 63); as *foveolate* (Fig. 20, B) when it is covered with shallow circular or polygonal depressions, each with the above-mentioned small vascular protuberance; as *areolate* (Fig. 20, C) when the depression is polygonal, more or less flat-bottomed and surrounded by a low, narrow ridge; as *fimbriate* (Fig. 20, D) when this ridge is higher, with the margin lacerate, denticulate or cut up into a number of short paleæ; as *setiferous* (Fig. 20, E) if the lacinix of the margin are long and narrow like the paleaceous setæ of the pappus; as *alveolate* (Fig. 20, F) if the ridge is higher still with the margin entire or variously divided.

In addition to these variations there is the *paleaceous* receptacle with membranous scales, each of which subtends a floret. The latter point is frequently ignored and the term paleaceous applied to the setiferous receptacle but, as Cassini and Goebel maintain, there is an essential difference between the paleaceous setæ, which surround the achene, and the paleæ, which occur in the positions of bracts.

Considering the origin of the capitulum from the racemose umbel, it is probable that the inner bracts were already very much reduced or entirely absent before the suppression of the pedicels. The appearance of scale bracts or other structures among the sessile florets would in that case be either reversion or a new development. The sporadic appearance of paleæ in the position of bracts in genera or even species with all their relatives non-paleaceous has all the characteristics of atavistic variation. The series of variations from the foveolate to the alveolate and setiferous types shows a progressive development of the ridge between the depressions which clearly constitutes successive stages in the development of secondary structures. Their secondary nature is confirmed by their first appearance after the formation of the gynœcium in the development of the capitulum (see Martin, II, 47, p. 355 and Pl. XIX, Fig. 9b).

The primitive receptacle would, therefore, be flat or nearly so and would show a foveolate structure, with reversion to a pre-Composite ancestor evident in the occasional appearance of paleæ in the positions of bracts, and with the subsequent development of the setiferous and alveolate types indicated by the occasional appearance of the fimbriate type.

C. ANALYSIS OF THE FORMS OF RECEPTACLE IN THE COMPOSITÆ.

As pointed out at the beginning of this chapter the evidence from all the other parts of the capitulum is so strongly in favour of the general scheme of evolution shown in Fig. 7 that the variation in the receptacle must be considered in relation to these other phyletic data.

Senecioneæ. These data clearly indicate the *Senecioneæ* as the basal sub-tribe and *Senecio* as the basal genus. The condition of the receptacle in that genus is, therefore, very interesting. Bentham (I, 8) describes it as flat or slightly convex, naked, foveolate or shortly fimbriate; this is quite in accordance with the conclusion arrived at in Section B, but the atavistic appearance of receptacular paleæ also occurs, e.g., occasionally in *Senecio* (*Senecillis*) *glauca*, Gaertn., Fig. 21. This anomaly has not previously been recorded in *Senecio* and adds one more to the numerous cases in this genus of variations which indicate the "critical tendencies" throughout the family, and which taken together leave very little doubt of the correctness of the view that *Senecio* is the basal genus of the *Compositæ*.

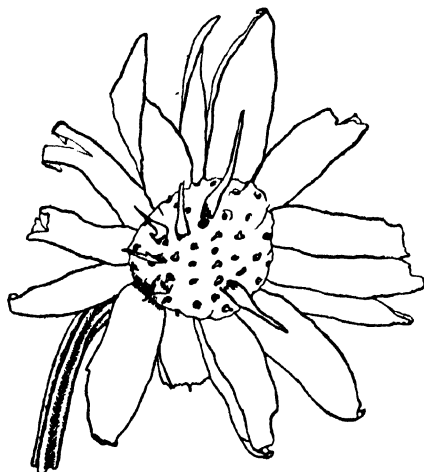


FIG. 21. Sub-biscriate involucre and paleaceous receptacle of *Senecio glauca*, Gaertn.; an abnormality in an authentic herbarium specimen. Magnification—about 3 diameters.

The receptacle in most of the *Senecioninæ* is flat and naked, but conical receptacles and foveoles occur in a number of genera and the fimbriate type in some species of at least six genera. *Raillardia* which has been removed on insufficient grounds to the *Helianthæ* by Hoffman has the receptacle setiferous; *Bartlettia* is more or less scrobiculate and *Arnica* is often villous. The range in the *Senecioninæ* is, therefore, that of all the more primitive forms of receptacle.

Fimbrillate alveoles occur in *Euryops* in the Othonninae but as a rule the receptacle is naked or foveolate both in that sub-tribe and the Tussilaginatae. The range in the Liabinae is interesting: *Liabum* is naked, alveolate or fimbrillate; *Gongrothamnus* (=Sect. IV of *Vernonia*, Hoffman) is foveolate; *Neurolaena* has caducous paleae and *Schistocarpha* deciduous paleae.

Vernoniae. The same amount of variation is shown by the Vernoniinae, where the receptacle is usually naked. In *Vernonia* it is naked, foveolate or fimbrillate. Foveoles occur in a few species of only two genera in the Lychnophorinae, the others having no appendages.

Cichorieae. All the receptacular forms occur in this tribe and, according to Bentham, have very little taxonomic value; the paleae when they occur are very thin, usually deciduous and not at all like bracts. Bentham (I, 7, p. 482) agrees that the Cichorieae are probably the most recent tribe, so that the sporadic appearance of paleaceous bracts is strong evidence of their atavistic nature.

Calenduleae. Practically without exception the receptacle here has no appendages.

Arctotideae. This tribe has the alveolate type well-developed; the margin of the alveole may be entire or variously divided. In *Ursinia* the alveole is divided almost or quite to the base so that each achene is surrounded by a number of narrow paleae, free or fused in a ring at the base. Three small genera show the naked or foveolate types, with, in *Haplocarpha*, a tendency to develop the fimbrillate form. The Gundeliinae are markedly setiferous, so that the relative positions of the sub-tribes and the primitive position of *Ursinia* are confirmed by the characters of the receptacle.

Anthemideae. The only distinction, and it is admittedly artificial, between the Anthemidinae and Chrysanthemidinae is the presence of receptacular paleae in the former and their absence in the latter. The latter sub-tribe has, as a rule, no appendages on the receptacle, but foveoles, fimbrillae, setae, alveoles and even a few short paleae occur in some of the genera, so that even this artificial distinction breaks down in a few cases. Reclassification on a natural basis is required.

Inuleae. The receptacle here has no appendages as a rule, but paleae occur in a few species in almost every sub-tribe and the other types occur so sporadically that few phyletic data can be obtained. It may be noted, however, that *Helichrysum* is naked, foveolate or alveolate and *Gnaphalium* naked or foveolate, so that the primitive receptacle occurs in the chief genera of the primitive sub-tribe.

The only other point of interest is the predominance of the setiferous type in the Bupthalthinæ where every genus shows an approach to this character, some with paleaceous bracts which surround the florets, others with the true setiferous form, cp. Cynareæ below. Bentham's remarks (1, 8, p. 337 sqq.) on two of these genera are of interest, especially as he considered the Inuleæ to have no real affinity with the Cynareæ (see Chap. I, Fig. 2) *Geigeria*, he says, has the receptacle and corolla of the Cynareæ; *Rhanterium* is stated to have the habit of *Centaurea* with the exception of the ray florets.

Cynareæ. The receptacle in all but three genera is setiferous, the setæ being slender, or flat and more or less paleaceous. The exceptions are *Berardia* and *IVarionia*, removed to the Mutisiæ by Hoffmann, and *Onopordon* in the Carduinæ, where the receptacle has foveoles or shallow alveoles with the margin more or less lacerate. This is so exceptional in the tribe that it is better regarded as a reversion, especially as *Onopordon* shows no other primitive characters.

Mutisiæ. The receptacle here is frequently naked or foveolate, paleæ occur in a few small scattered genera. The condition in *Trixis* is of interest (cp. Chap. V), the receptacle is naked or fimbriate, the fimbriæ being very slender. This is quite in accordance with the primitive position suggested for that genus. No difference in the condition of the receptacle can be traced as distinguishing the various sub-tribes.

Astereæ. The Homochrominæ and Heterochrominæ show a scattered distribution of all the receptacular forms. The Bellidinæ and practically all the Grangeinæ have no appendages. The Conyzinæ are naked, foveolate or fimbriate and the setiferous form in addition to these appears in the Baccharidinæ.

Eupatoriæ. The receptacle here is usually naked but is pubescent in a few genera and alveolate in *Hofmeisteria*. Caducous or deciduous paleæ occur occasionally in eight genera, which are mostly small or monotypic.

Helianthæ. The normal condition of the receptacle in this tribe is paleaceous. The paleæ may be broad and persistent, or narrow and more or less deciduous, subtending the florets: there may be as many scales as there are florets or, as is frequently the case, the scales may be reduced or absent in the centre of the capitulum, or as in many other cases the paleæ may be narrow and more numerous than the florets, surrounding, not subtending, them.

As the *Helianthæ* are an advanced tribe in practically every other character of the capitulum, it is obvious that the paleaceous receptacle is not the primitive character which it has been assumed to be by Bentham (I, 7, p. 482) and others, but is partly the expression of a tendency to revert to a pre-Composite ancestor (which tendency is present in *Senecio* but attains its highest development in this tribe) and partly the expression of the tendency of the foveoles to develop into the setiferous form.

The return to the normal condition for the family takes place at the end of the Coreopsidinean line in the *Milleriinae* where paleæ are seldom present and the receptacle has normally no appendages. The *Lagasceinae* also show no appendages. All the other tribes have paleæ either subtending or surrounding the florets in practically every genus.

Heleniæ. As this is one of the few tribes from which floret-subtending paleæ are completely absent, the relationship of the *Galinsoginae* and *Tagetinae* requires examination. The receptacle in the latter sub-tribe is usually naked or flimbrillate and is alveolate with lacerate alveole margins in *Adenophyllum*. At least three of the genera of the former sub-tribe have the paleæ more numerous than the florets and more or less connate in lacerate alveoles. As one of the three is *Calea*, the chief genus of the sub-tribe, corroboration of the previously suggested affinity is obtained when the receptacle is examined in detail. The *Heleniæ*, therefore, are an end group with no paleæ, corresponding to the non-paleaceous *Milleriinae* on the other main evolutionary line of the *Helianthæ* (cp. Fig. 7). The *Jaumeinae* and *Flaveriinae* have no receptacular appendages; the *Heleniinae* have appendages only in two genera, long setæ in *Gaillardia* and foveoles in some species of *Hymenoxys*. The *Baeriinae* are usually naked, but show all the types except the paleaceous receptacle.

D. THE PHYLOGENETIC SIGNIFICANCE OF THE RECEPTACLE.

The receptacle, like the pappus and involucre, is of doubtful taxonomic value, but the critical tendencies shown by the primitive tribe again give the clue to the phyletic interpretation of the variations. Taking the alveolate and setiferous types as advanced, the foveolate and naked forms as primitive and the receptacular paleæ when they subtend florets as reversions to a pre-Composite ancestor, the variations shown by the receptacle confirm in one or two points the previous phyletic conclusions, while the rest of the data are not opposed to these conclusions.

The *Senecioninæ* and *Senecio* are confirmed as basal; the *Liabinæ* are confirmed as the source of the *Vernoniinæ*. The evidence is in favour of *Ursinia* being the primitive genus of the *Arctotideæ* and of the position of the *Gundeliinæ* as in Fig. 7. In the *Inuleæ* the primitive position of the *Gnaphaliinæ* and the *Buphthalminæ* as the source of the *Cynareæ* are confirmed.

The need for reclassification of the *Cichorieæ* and *Anthemideæ* on a natural basis is again emphasised.

The position of *Trixis* at the base of the *Nassauviinæ* is strengthened. The position of the *Heliantheæ* above the *Senecioneæ*, the position of the *Milleriinæ* and the derivation of the *Tagetinæ* from the *Galinsoginæ* are all confirmed.

The receptacle, therefore, although of little taxonomic or phyletic value furnishes evidence in favour of the suggested origin of several tribes, *viz.*, *Cynareæ*, *Heliantheæ*, *Heleniæ*, *Mutisiæ* and *Arctotideæ*.

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CHAPTER VIII.

PHYLLOTAXIS OF THE COMPOSITÆ.

THE vegetative part of the plant in the Compositæ varies so markedly that it is of little use in taxonomy or phylogeny apart from the special vegetative organs of the capitulum which have been considered in Chapters VI and VII. Nevertheless it is of interest to consider the occurrence of opposite and alternate leaves throughout the family, as even this variable character agrees in several points with previous phyletic conclusions; this is done in Section B. In addition the phyllotaxis of the capitulum is of considerable interest and is discussed in Section A of the present chapter. A brief summary of the phyletic data obtained in the study of the phyllotaxis of the family is given in Section C.

A. PHYLLOTAXIS OF THE CAPITULUM.

The variation of the number of the ray florets in the Compositæ, being easily observed, has furnished a basis for much of the work on the significance of the Fibonacci series.

History. For a full account of the salient features in the history of phyllotaxis in general, readers are referred to Church (1, Pt. I). Wydler (29) seems to have been the first to consider phyllotaxis in the Compositæ in any detail and he gives the data for the capitula and leaves of many species. Ludwig (15-18) gives maxima for the ray florets at 5, 8, 13, 21 and others of the Fibonacci series. He used the Schimper-Braun accessory series to explain the secondary and tertiary modes observed (18). A little later Haacke (6) found similar monomodal variation curves, but the modes in many cases did not fall in the Fibonacci series and from his data he concluded that the number of rays florets varied with the locality and the nutrition of the plants. Haacke thus anticipated the modern work on place-constants and seasonal variation.

About the same time Weisse (25) published a long account of the phenomenon, with a good bibliography and a summary of the periodicity theory as given by Ludwig. Weisse also considered the phyllotaxis of the disc florets, describing it in terms of curve systems (cp. Church). He pointed out that the rays come at the ends of the long curves, *e.g.*, a capitulum with a 21 : 34 curve system has 21 rays. He agreed with Haacke in regarding the multimodal curves obtained from uncultivated material as due to nutrition and not to the presence of true races. This same author has also given a brief account (26) of Schwendener's mechanical theory of

phyllotaxis. Church (1, Pt. I, p. 16) remarks of this theory that "it superimposes a second doubtful hypothesis on the original unsatisfactory one of Schimper and Braun."

Most of the more modern work agrees in finding seasonal and local changes in the number of ray florets, the modes not being confined to the Fibonacci series (see VI 13, VI 14 ; 5, 12, 13, 14, 19, 23, 24, 27). Strickland (22) in one of the most recent notes on the subject returned to the concentric circles of the Schimper-Braun hypothesis, but was answered within a month by Henslow (11), who referred to his own observations on phyllotaxis (7-10). In spite of the variation observed, a monomodal curve with the mode at 21 is very common in the *Compositæ* (cp. 20, 28).

Church's work. This author, in addition to various notes (2-4) on the simpler aspects of phyllotaxis, has published the most complete exposition of phyllotaxis in general and of the phyllotaxis of the capitulum in particular (1). Some of the points explained by Church which are directly relevant will now be given, but as the phyletic value in the *Compositæ* of these very interesting data is rather restricted readers are referred to the original for details. Indeed, for the proper comprehension of what occurs in the capitulum a close study of Church's monograph is essential and all previous work may be regarded as more or less superficial when compared with that author's fundamental exposition of the subject.

Involucre. The involucre scales, according to Church, show a "rising phyllotaxis" and the phyllotaxis cannot, here or elsewhere in the capitulum, be given a real value in the fractional system of Schimper and Braun. In dealing with the phyllotaxis of *Helianthus* (op. cit., Pt. I, p. 25) he says "the vegetative leaves pass gradually by reduction into an involucre of leaf-base scales." The study of the phyllotaxis of the capitulum confirms, therefore, the theory of the origin of the calyculus from the cauline leaves by suppression of the internodes (cp. Chap. VI).

In *Helianthus* the difference between the uniseriate pericline and the multiseriate calyculus is very distinct. Taking the case figured (op. cit., Pt. II, Fig. 50), the whole plant shows a rising phyllotaxis, from the (3 + 5) of the foliage leaves and the (8 + 13) of the foliage leaves and calyculus to the (21 + 34) of the disc. The transition from the (3 + 5) of the lower cauline leaves to the (8 + 13) of the upper foliage leaves and calyculus occurs below the calyculus so that the leaves of that part of the capitulum have the same phyllotaxis as the upper foliage leaves. The passage of the foliage

leaves into the calyculus is, therefore, gradual. The passage from the $(8 + 13)$ system of the calyculus into the $(21 + 34)$ of the disc occurs in the pericline, the 21 members of which are transitional and subtend the 21 ray florets at the ends of the long spirals.

In the cases mentioned in Chap. VI, B, where the calyculus passes gradually into the pericline the change from the lower to the higher curve system is not accomplished in the minimum number of members as it is in *Helianthus* and the transition begins with the inner members of the calyculus and continues in the outer members of the pericline. The two parts of the involucre in these cases belong to the same curve system and appear, therefore, to pass gradually into each other.

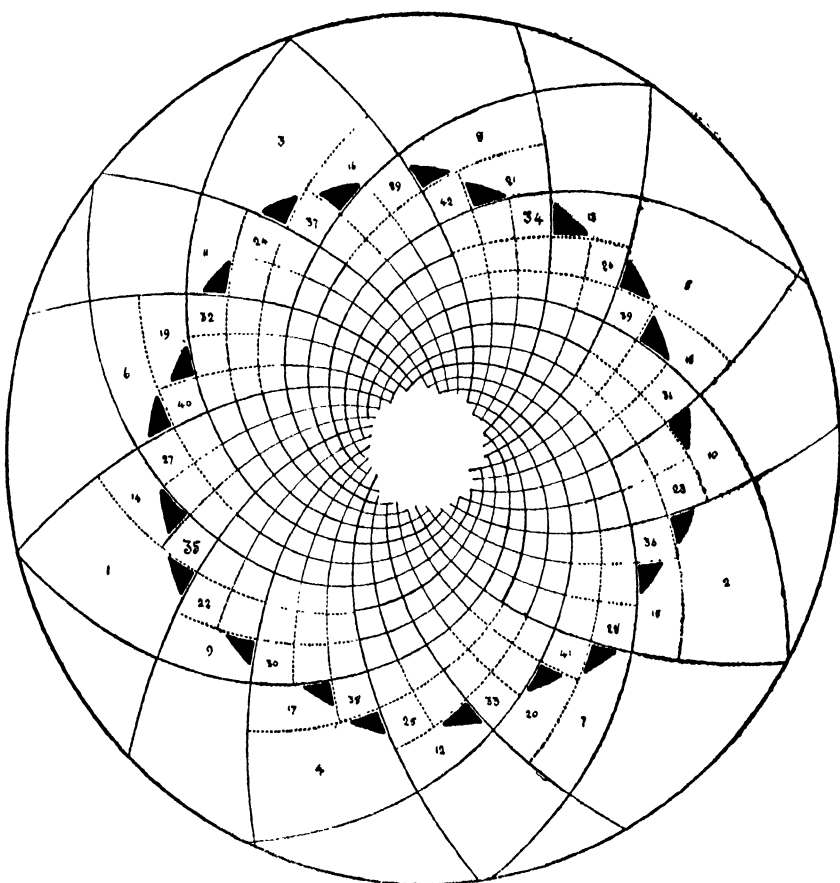


FIG. 22. Expansion system: log. spiral scheme for the introduction of new paths which determine the rise of phyllotaxis ratios in the capitulum of *Helianthus annuus* from $(8 + 13)$ to $(21 + 34)$. A small capitulum is taken as a type; the genetic spiral winds left; the small amount of unavoidable error in the construction is admitted in the $(8 + 13)$ system. (Figure and legend after Church).

Another case is exemplified by *Cynara Scolymus* (op. cit., Pt. II, p. 119) where the distinction between the foliage leaves and

calculus is very marked, as is the case in most *Compositæ*. Here there is one transition from the foliage leaves (3+5) to the "outer involucre" (8+13), a second transition from the "outer involucre" to the "inner involucre" (21+34) and a third to the disc florets (55 + 89). The outer and inner parts of the involucre may be considered calculus and pericline respectively and the transition which occurs to give the calculus marks off the involucre very definitely from the cauline leaves.

These few examples will be sufficient to show that the morphological distinction drawn between the two parts of the involucre is confirmed by the phyllotaxis.

Ray Florets. Most of the work on the phyllotaxis and biometrics of the capitulum has been done on the ray florets and one of the most interesting points in the whole of the literature of phyllotaxis is the geometrical construction given by Church, which explains the number and position of the rays. The chief points can be seen in Fig. 22,¹—for the method of construction the reader is referred to the original monograph (1, Pt. II, pp. 116 sqq.). The method consists in adding one long and one short curve to each of the first 13 members of the (8 + 13) cycle and one short curve to the remaining 8 members of the complete cycle.

The ray florets are marked black and it will be seen that they fill in the corners left by the transitional members of the involucre or pericline which are all more oblong than square and thus differ from the quasi-squares of the disc and the outer involucral members or calculus. The members of the pericline are thus quite definitely indicated and it will be noted that according to this construction the ray florets are always more or less to one side of the subtending bract. This displacement of the floret from the median position is more marked with the outer bracts. It should also be noted that the ray florets occur at the ends of the long spirals, *e.g.*, there are no rays at the ends of the short spirals marked 22, 25, 30, etc. Starting from the bract numbered 1 (Fig. 22) and counting from left to right round the lower part of the circle it will be noticed that the ray florets are grouped thus 2 : 1 : 2 : 1 : 2 : 2 : 1 : 2 : 1 : 2 : 2 : 1 : 2. As there are 21 long spirals there are 21 ray florets, so that the number and position of the rays follows from the geometrical construction adopted.

¹ I am much indebted to Dr. A. H. Church for his kindness in lending me the blocks for Figs. 22-24, which are Figs. 44-46 in the original.

That this is not merely mathematical twisting of facts to suit the construction can be seen from Figs. 23-24. The occurrence of individual capitula with 22 rays involves abnormalities in the system and such a case is shown between the bracts numbered 21 and 34 in Fig. 24 (cp. Fig. 23).

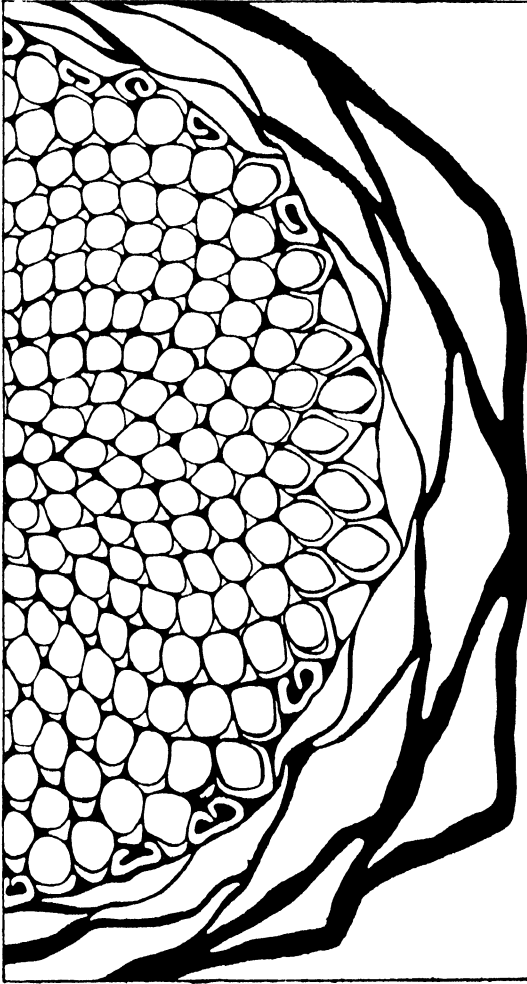


FIG. 23. *Helianthus annuus*. Section of a young capitulum, 10mm. in diameter: cam. lucid. drawing of half the disk (Figure and legend after Church.)

Similar figures can be drawn for heads with 13, 34 or more rays and are widely different from the artificial figures given by Schwendener and Strickland.

Disc Florets. The theoretical arrangement of the disc florets according to the $(21+34)$ curve system is illustrated in Fig. 22, but, just as rising phyllotaxis characterises the involucre, so falling phyllotaxis characterises the centre of the capitulum. The spirals of the $(21+34)$ system are true to nature up to a point where the size of the floret requires some accommodation in the arrangement. This is necessary because all the florets mature more less simultan-

eously and are of similar dimensions, whereas the space for each floret in the geometrical system grows gradually smaller.

The fall does not appear to take place with the same regularity as the rise, but the Fibonacci ratios occur and mark positions of relative stability in the progress of the fall. The 21 long spirals continue, but the 34 short spirals become approximately 13; these would become the long spirals of the $(13 + 21)$ curve system of the centre.

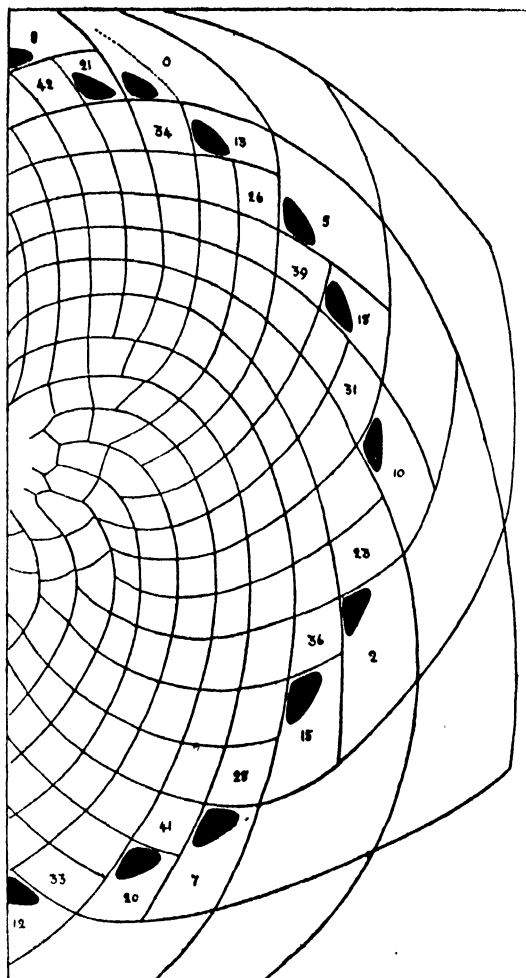


FIG. 24. Curve-tracing of the preceding. the ray florets are blocked in and the areas numbered in agreement with the theoretical construction of Fig. 22. (Figure and legend after Church.)

In the upper half of Fig. 24 a tendency to the same $2:1:2:1:2$ arrangement of the spirals as occurs in the rising phyllotaxis can be seen. Church gives photographs of capitula in which the falling phyllotaxis of the centre of the disc is more distinct, but observations can be made with most facility on actual fruiting heads of the sunflower and more than one "falling" transition can sometimes be distinguished.

Bijugate Types. In the normal Fibonacci phyllotaxis a single genetic spiral can be traced. This, however, is quite a subjective phenomenon. Other cases occur with two or more genetic spirals and these are described as bijugate or multijugate. Where the capitula are bijugate the phenomenon usually extends to the vegetative parts and the leaves then occur in pairs which may or may not decussate.

This bijugate phyllotaxis is amenable to the same geometrical treatment by means of curve systems of the series $2(5+8)$ or $(10+16)$ etc., (cp. I, Pt. II, p. 166). Bijugate systems occur rarely in *Helianthus annuus* and are also normal in the terminal capitula of some species, e.g., *Silphium perfoliatum*, where the lateral capitula show the normal Fibonacci phyllotaxis. Other cases in the Compositæ which are sometimes bijugate are *Arnica*, *Spilanthes* and *Zinnia*.

B. PHYLLOTAXIS OF THE LEAVES.

Wydler (29) and Reinecke (21) give numerous data of the phyllotaxis of the vegetative parts of the plant. Cassini (I, 18) confined his attention with very excellent results to the floral characters of the family. Bentham (I, 7) gives a short and not very accurate analysis of the distribution of alternate and opposite leaves in the various tribes.

That opposite leaves are primitive in the Dicotyledons is fairly obvious from the condition of the embryo and is proved by Henslow (8). The addition of one extra member, giving a $(2+3)$ system instead of a $(2+2)$ system is considered by Church to take place very readily, so that an alternate phyllotaxis probably arose at an early stage in the history of the Dicotyledons (cp. Henslow, *loc. cit.*).

The fact that opposite leaves are primitive for the Dicotyledons is, therefore, quite irrelevant, and the evidence within the Compositæ is in favour of alternate leaves being the primitive condition for the family. The probable origin of the Compositæ from the Lobelioideæ, where the leaves are practically always alternate, furnishes further evidence.

As the distribution of these two types of phyllotaxis follows the general phyletic lines already laid down, a brief account of the variation will add to the cumulative effect of the evidence for these phylogenetic conclusions.

As before, the Senecioninæ show the primitive type (alternate) with variation showing reversion to the type which doubtless was

primitive in a very distant ancestor. Opposite leaves occur in *Arnica*, *Gynoxys* and *Haploesthes*, which are close relatives of *Senecio*. The Liabinæ have alternate leaves in two genera and opposite leaves in the others. The other genera of the Senecioneæ are all alternate with the exception of *Raillardia* where the phyllotaxis varies.

The Cichorieæ are without exception alternate. The Calenduleæ are almost all alternate, but *Tripteris* and *Osteospermum* show opposite leaves occasionally. A similar condition occurs in the Arctotideæ, where *Berkheya* and *Didelta* in the Gorteriinæ have opposite leaves in a few species. As the Arctotidinæ are primitive this occurrence of opposite leaves in the Gorteriinæ is one small piece of evidence in favour of that phyllotaxis being atavistic in the Compositæ.

Alternate leaves are the rule in the Anthemideæ but at least six genera, mostly monotypic, are opposite-leaved.

In the Inuleæ opposite leaves occur occasionally or always in one or two genera in each of the sub-tribes, Gnaphaliinæ, Angianthinæ, Relhaniinæ, Athrixiinæ and there are no exceptions to the alternate phyllotaxis in the other five tribes, including the Bupththalmiæ and Plucheinæ. This fact is of interest as there is also no exception to the alternate phyllotaxis in the Cynareæ, another small point which adds its quota to the evidence for the derivation of the Cynareæ from the Bupththalmiæ or Plucheinæ.

The distribution in the Mutisieæ also supports the idea of the opposite phyllotaxis being atavistic. It is absent in the primitive sub-tribe, Nassauviinæ and occurs occasionally in one genus of the sub-tribes, Gerberinæ, Onoseridinæ and Barnadesiinæ and in two genera of the Gochnatiinæ.

The occasional appearance of opposite leaves in the Vernoniinæ, including *Vernonia*, is in accordance with the predominance of that character in the ancestral group, Liabinæ.

At least nine genera of the Eupatorieæ have always alternate leaves; in at least eight others, including *Eupatorium*, the upper leaves are sometimes or always alternate, while the lower leaves are opposite. The other genera, about fifteen, are always opposite-leaved. This condition makes the examination of the Astereæ interesting. There alternate phyllotaxis is the rule with no exceptions in the Conyzinæ and Bellidinæ. In the Homochrominæ opposite leaves occur occasionally in *Pentachæte*, *Lepidophyllum* and in most of the species of *Pteronia* (cp. Hutchinson, VI, 9). In one genus each of the Grangeinæ and Baccharidinæ the leaves are rarely sub-opposite. In the Heterochrominæ the leaves are rarely

opposite in *Olearia*, and the normal condition with opposite lower leaves and alternate upper leaves in *Amellus* is particularly interesting in view of the probable origin of the Eupatorieæ from the Heterochrominæ.

The Heliantheæ although advanced in all their floral characters show atavistic tendencies in the phyllotaxis as well as in the receptacle. Most of the Verbesininæ show opposite phyllotaxis either entirely or only in the lower leaves. About a dozen small genera are always alternate throughout. Alternate leaves are the rule with a few exceptions in the Ambrosiinæ and Petrobiinæ. Opposite leaves are the rule with a few exceptions in the Lagasceinæ, Zinniinæ, Milleriinæ and Coreopsidinæ. About two-thirds of the Melampodiinæ are opposite, the rest being alternate (cp. the Milleriinæ line in Fig. 7). The Madiinæ are alternate without exception and the condition in the Galinsoginæ is of particular interest. Here, as in the Heleniæ, about half of the genera show one type and the other half the other type.

The detailed distribution in the Heleniæ is also of interest; the two types occur in almost equal proportions in the Tagetinæ and Baeriinæ; opposite leaves are the rule with one exception in the Flaveriinæ and alternate leaves the rule without exception in the Heleniinæ, cp. Fig. 7.

C. PHYLOGENETIC SIGNIFICANCE OF PHYLLOTAXIS.

The study of the detailed phyllotaxis of the capitulum yields several important phyletic data; the calyculus is proved to be more akin to cauline leaves than to the periclinal bracts; the distinction drawn between these two parts of the involucre in Chap. VI. is upheld; the number and position of the ray florets is proved to be primarily dependent on the bracts of the pericline; the uniseriate type of ray is seen to be the primitive condition in radiate capitula, but the balance of the evidence is still in favour of the discoid capitulum being primitive for the family.

The analysis of the phyllotaxis of the leaves in so far as they are opposite or alternate supplies phyletic evidence which, although of no great value, is of considerable interest in that it follows in some detail the phyletic lines already elucidated.

The most interesting points are noted in Sect. B so that it is only necessary to direct special attention to the phyllotaxis of the Senecioninæ, Liabinæ and Vernoniæ; the Nassauviinæ and the rest of the Mutisieæ; Bupthalthminæ and Cynareæ; the Heterochrominæ and Eupatorieæ; the Galinsoginæ and Tagetinæ; and the marked atavistic tendency in the Heliantheæ which is in accordance with the other atavistic tendencies in that tribe.

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CHAPTER IX.

FRUIT DISPERSAL IN THE COMPOSITÆ.

ALTHOUGH there is a considerable variety of fruits in the family which are dispersed by animals, the chief dispersal mechanism is the pappus. The structure and evolution of this organ is dealt with in Chap. V. Its efficiency as a dispersal mechanism has been questioned by a number of observers and experimenters; it was considered necessary, therefore, to investigate the problem experimentally, and the method and results are given in Section B of the present chapter, after the brief account of previous records in Section A. As the experimental results are somewhat at variance with accepted views the hydrodynamics of the simplest case are discussed in Section C. The bearing of the results on the problem of the development of the family is indicated in the last section of the chapter.

A. HISTORY.

The dispersal of seeds and fruits has been the subject of many observations. The literature of the subject was dealt with by Hildebrand (V, 32), and again by Hemsley (23). A further index of the literature from 1873 to 1890 is given by MacLeod (27), and a more recent bibliography by Sernander (33), who refers to Linné's *Oratio de telluris habitabilis incremento* of 1743 as the beginning of the study of plant dispersal. As there is a readily available account of the general phenomena with a good bibliography by Praeger (30) only special points will be mentioned.

Cassini (8) was one of the first to consider fruit dispersal in the Compositæ, and he differentiated eight methods by which the fruits are liberated from the capitulum. De Candolle (11) gave details of many species, and pointed out that many wide-spread species have no pappus. He formed the opinion that the pappus was effective as a means of dispersal for short distances only, *i.e.*, up to half-a-mile. Hildebrand (V, 30) considered the various modifications in the fruit in relation to their dispersal, and gave examples from the Compositæ in his general treatise, and also in a previous account of hooked fruits (V, 31). Bentham gave a short

general account (I, 7, p. 572), but laid great stress on the colonising powers of the Compositæ apart from their dispersal mechanisms. Wallace (41) explains the anomalous distribution of certain Compositæ by their "great powers of dispersal," and in Chap. XXIII gives some details of the general migration from north to south along the mountain ranges. More recent observations by Guppy (21-22) and Praeger (30) emphasise the importance of ocean currents and birds as means of dispersal.

A curious point is raised in the consideration of the dispersal of the radiate variety of *Senecio vulgaris*. Professor Trow informs me that although it is possible that the radiate character was introduced into Great Britain from the Channel Islands it would be more correct to speak of the spread of the character "radiate" than of the radiate variety. The records of radiate groundsels are records of the character but are not necessarily records of the same variety.

Dispersal by Animals.

Dispersal by birds for comparatively long distances is given by Darwin (II, 16), Wallace (41), Hemsley (23), Guppy (21), Praeger (30) and others. The fruits during dispersal may be either inside the bird (in the crop or elsewhere) or outside the bird amongst its feathers or among the mud which occasionally adheres to the feet.

Adherence of the fruit may be obtained by glandular structures, as in *Adenostemma*, *Siegesbeckia* and *Wulffia* (V, 30; IV, 98) or by mucilaginous pericarps, as in *Rutidosis* (V, 14), *Chrysanthemum Fontanesii*, *Ruckeria* and *Trichocline* (V, 32), and also in *Chrysanthemum multicaule* as observed by the writer. Adherence may be obtained also by hooks, as in many genera; the hooks being on the involucre, as in *Arctium* and *Xanthium*, or on the pappus, as in *Bidens*. These cases and several others are mentioned by De Candolle (11), Hildebrand (V, 30-32), Kronfeld (VII, 3), Huth (V, 41) and others.

Dispersal by man has been mentioned only in passing by most botanists, but is the subject of a paper by Thellung (34) who mentions a number of Compositæ which have been dispersed as weeds or as horticultural plants. This rather neglected branch of fruit dispersal is most interesting on account of the many traditions with which it is connected, such as the reputed introduction of "Stinking Willie" (*Senecio Jacobæa*) into Scotland in the fodder of the German cavalry used by William, Duke of

Cumberland. Such material is, however, pabulum for the philologist and archæologist rather than the botanist.

Dispersal by Water.

Among the first observations of fruit dispersal in the Compositæ is a series of experiments by Hoffmann (24) on the floating powers of a number of species, most of which sank within twenty days. De Candolle (11) and Hemsley (23) give rivers and ocean currents as agents which disperse fruits to great distances, but no case of such dispersal in the Compositæ is quoted, although dispersal on floating logs and icebergs, as mentioned by Darwin (11, 16) and Guppy (22), is quite possible. Kronfeld (VII, 3) showed that pappus fruits such as those of the dandelion float much longer with the pappus attached, even when it is closed. The closed pappus usually surrounds an air bubble which assists in the flotation.

In the case of Krakatau (15) some of the species of *Wedelia* and possibly also those of *Conyza* and *Blumea* were transported by ocean currents, and in the somewhat similar case of Taal Volcano (19-20) *Wedelia biflora* and *Eclipta alba* most probably arrived by water. The latest addition to the meagre list of water-dispersed Compositæ is *Ambrosia crithmifolia*, which is given by Guppy (22) as transported on drifting logs.

Dispersal by Wind.

The pappus has usually been regarded as an efficient mechanism for dispersal by wind, and there have been many general observations of the structure on this account, such as those of Hildebrand (V, 30-32), who also mentions cases (V, 30) of wind dispersal of the whole capitulum where the involucre bracts act as wings. Kronfeld (VII, 3) considered that in the case of *Tragopogon pratensis* the lateral cilia of the setæ produce a structure which acts as if it were a continuous membrane. Taliew (V, 65), Steinbrinck (V, 64), Hirsch (V, 33), Frieb (18) and others have noted the biological significance of the hygroscopic movements of the setæ and involucre bracts, dispersal being favoured by dry winds and prevented by moist winds.

Poerste (17) mentions a curious addition to the dispersal mechanism in *Ambrosia trifida*. The achenes are beaked, with five short protuberances at the base, and five or six strands of ice have been observed attached to these on frosty mornings: as these "ice-curles" were 1½ to 3 inches long Poerste suggests that they aid

the wind dispersal of the fruits. Another curious but better known anomaly is the dispersal mechanism of *Parthenium hysterophorus*. Here the bracts enclosing two male florets are attached to the top of the achene of each female floret, and these bracts with the withered male florets enclosed act as wings.

The mechanics of the pappus have been considered by Dingler (12), Praeger (30), Mattei (28) and Dandeno (9), who all regard the mechanism as a simple parachute.

Apart from these general observations there is the controversial question of the distance to which a pappose fruit can be dispersed by the wind. De Candolle (11), although he regarded the wind as "la cause la plus générale et la plus ordinaire de dissémination des espèces sur toute la surface d'un pays," maintained that there was no evidence for the transportation of seeds over even narrow arms of the sea. He was, moreover, sceptical about the records of grains of sand, etc., being blown for long distances by the wind. Bentham (I, 7) also considered that a few miles was the limit for the dispersal of pappose fruits even by strong winds. Kerner (25), and more recently Beauverd (1), have shown that in the Alps pappose fruits are raised to a considerable height, but they both consider that all such fruits fall when the upward current fails in the evening, and that they come to rest very close to their starting point.

Praeger (30), with whom Guppy (22) agrees, calculates from the rate of fall in quiet air that many pappose fruits would require an initial elevation of about one mile before they could be blown to a distance of fifty miles by a wind of 50 m.p.h. Heavier fruits would require a still greater elevation according to Praeger. Willis, although he states (IV, 94) that the Orchids and Compositæ are best suited for long distance dispersal, and considers that wind-carried seeds arrive more frequently than other Angiosperms on hill-tops, maintains as a result of his observations on hill-top floras (43-45) that such cases of long distance dispersal are rare even in the Composite, and that "we have little evidence to show that it occurs for instance between one continent and another."

In spite of the objection of lack of evidence for long distance dispersal which is raised repeatedly by the above-mentioned authors, the positive evidence for such dispersal makes a longer list, and has secured more adherents than the view of the opposition. Wallace, for instance, in his "Island Life" says, "we are as

sure that seeds must be carried to great distances as if we had seen them so carried," and he furnishes a very good argument against the negative observations of De Candolle (who relied chiefly on the statements of the sailors that they had seen insects but not seeds blown long distances out to sea), and Kerner (who examined some part of the surface of a glacier but found no seeds other than local species). Wallace points out that if "every year a million seeds were brought by the wind to the British Isles from the continent, this would be only ten to a square mile, and the observation of a life-time might never detect one; yet a hundredth part of this number would serve in a few centuries to stock an island like Britain with a great variety of continental plants." He also notes that the arrival of seeds and colonisation are different matters; seeds arriving on ground already fully occupied would require more than a wind-dispersal mechanism to enable them to compete successfully with the established inhabitants.

Beccari (2) gives evidence for the dispersal of seeds for distances of 1000-2000 miles, *e.g.*, *Nepenthes ampullaria* from Ceylon to the Seychelles, but does not mention any special Compositæ. Similarly Engler (14) gives fourteen species of Angiosperms as transported by wind to the Sandwich Islands, but excludes the Compositæ on account of the width of sea to be crossed. Warming (42) also supports wind-dispersal to a distance of at least sixteen miles for quite heavy fruits. The distance is increased by Vogler's observations (38-40), but this author points out that, although wind-dispersal of seeds is possible up to 100 kilometres, more importance is to be attached to such dispersal for 3-20 kilometres and to the possibility of dispersal over high mountain ranges. Kronfeld (26) considers the rapid dispersal of various introduced Composites to be due to the efficiency of the pappus. Ridley (31) also considers that plumed fruits "can at least occasionally cross successfully large areas of sea," but points out that dense forests present an obstacle to the free dispersal of pappose fruits. Further confirmation of the efficiency of the pappus is given by Bessey (6). Schimper (32, p. 80), after giving the views of De Candolle and Kerner, quotes the case of Krakatau as evidence of wind-dispersal for twenty miles over the sea, and considers that "the significance of anemophilous means of dispersal in relation to the origin of an insular flora has been finally determined by Treub's important observations."

The case of Krakatau is of special interest since, of the eight

angiospermous species found by Treub (36) in the interior of the island and not on the strand three years after the eruption, four species were Compositæ: *Wollastonia* (= *Wedelia*) sp., *Conyza angustifolia*, *C. indica* and an unidentified species of *Senecio*. In the absence of other evidence it is at least possible that this "Senecio" of Treub was *Emilia sonchifolia*, which is very like a *Senecio*, and which was found by Penzig (29). No *Senecio* was found by either Penzig or Ernst (15). The former found five and the latter eight Compositæ, of which *Blumea balsamifera* and *Vernonia cinerea* were found by both and *Emilia sonchifolia* only by Penzig in 1897, fourteen years after the eruption.

These three species are particularly interesting as they occur again in the list of ten species of Compositæ found by Gates (19) on Taal Island (in Bombon Lake, Luzon) about three years after an eruption there which denuded the island of vegetation. The re-vegetation was naturally more rapid than on Krakatau as the source of the seeds was about 6 km. instead of about 18 km. distant. In both cases a number of Compositæ were strand plants, evidently dispersed by ocean currents, but on Krakatau four species of Compositæ were undoubtedly transported by the wind, and at least seven species on Taal were probably wind-borne, two (*Blumea* sp. and *Pterocaulon cylindrostachyum*) occurring only on the crests of mountain ridges and the other five elsewhere in the interior.

The evidence from Krakatau is, therefore, confirmed by the observations on Taal Island, and there remains no doubt whatever of the usual dispersal by wind of a number of Compositæ to distances of 4-20 miles and the occasional dispersal of pappose fruits to distances of over 100 miles.

B. EXPERIMENTAL WIND-DISPERSAL.

There is apparently no record in which wind of a known velocity has been used in the experimental dispersal of pappose fruits; all the experiments have been done on the rate of fall in quiet air. It is, therefore, considered advisable to give some details of the apparatus and method used in the present investigation. The apparatus and method were demonstrated to Sect. K of the British Association in 1916, and to the Linnean Society in the same year (33a).

Apparatus.

The source of the wind was an electric fan (Fig. 25, A)

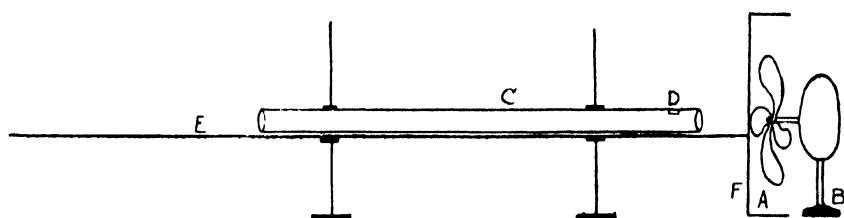


FIG. 25. Wind Dispersal Apparatus.

attached to a small motor B; by means of different resistances the speed of the fan could be varied. In the results given below Speed 1 is the slowest and Speed 4 the fastest. A wooden guard F, covered on one side with a net, surrounded the fan.

The fruits were blown through a glass tube C. As it was found that the wind eddied at the near end of the tube, a hole D, 2 cms. long and 1 cm. wide, was cut in the tube at a distance of 5 cms. from the end; through this hole fruits were dropped. As the whole length of the tube was 132 cms., this gave 125 cms. as the length for dispersal. A two-meter rule E was used, but as it was placed against the net 3.5 cms. were added to the readings to get the distance from the boss of the fan. This accounts for the constant occurrence of this number in the figures given below.

Anemometer.—The wind pressure was measured by means of an anemometer designed for the purpose. The ordinary rotating anemometer is empirical and not accurate for slow speeds (cp. 7), and further it was more important to obtain a measure of the pressure of the wind on a surface somewhat similar to that of the pappus than to obtain an empirical measure of the velocity of the air moving through the tube.

The anemometer (see Fig. 26) consists of a thin circular disc of tin A against which the wind impinges. The disc is accurately balanced by a ball of solder B on the other end of the top of the T beam. The horizontal part C of the beam is a thin steel rod, soldered to a flat strip of tin which forms the vertical part D of the T. At the base of D are a needle indicator E and a small hook F. The whole of the T beam is accurately balanced by means of solder on the back of D, so that when balanced on the watch-wheel fixed to D at G it remains in any position in which it is placed. In the instrument this T beam is balanced by the steel axis of the watch-wheel on adjustable agate edges at H and K. It is therefore free to move in any direction with a negligible friction when acted upon by a small force.

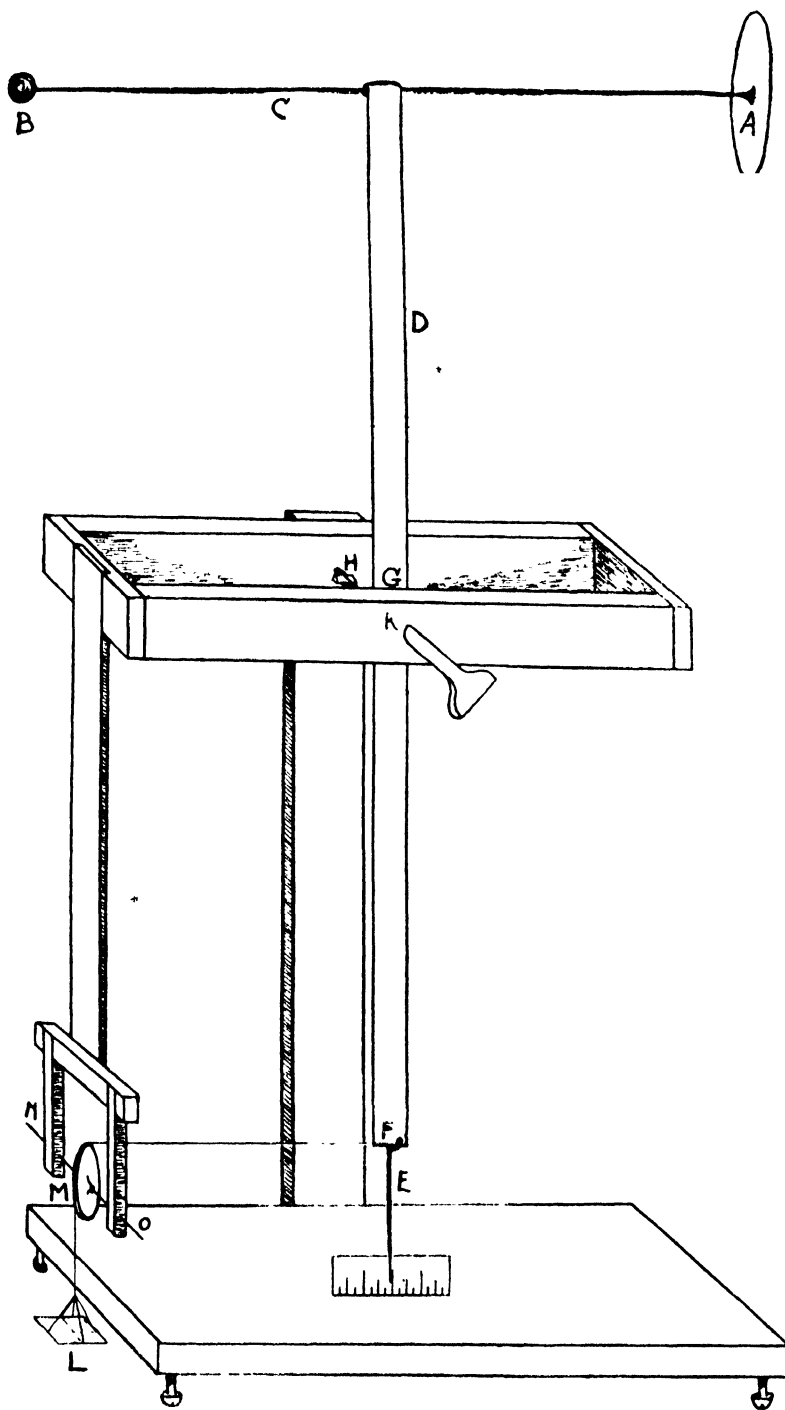


FIG. 26. The Anemometer.

The pressure of the wind on A is balanced by weights placed on a scale pan L. The scale pan is a small glass microscope cover-slip, hung by thread over a pulley M ; the thread is attached to the

hook F. The whole apparatus then acts as a simple mechanical couple. The hook F is the same distance from the fulcrum G as the top of the T beam, so that the weight on the scale pan and the weight of the thread, together with that of the scale pan itself, give a direct measure of the total pressure on the disc A. The pulley M has practically no friction, being a small brass wheel running on steel needle points. These needles N and O are adjustable, and when in proper condition the wheel runs for quite half a minute with no sound when given a slight touch. This practically frictionless pulley and the axis at G, which is balanced on sharp agate edges, are the only two points at which friction might cause an error.

When in use with the tube the disc of the anemometer was inserted a short distance into the tube, and as the diameter of the disc is 3.3 cms., and that of the tube is 4.5 cms., the conditions were very similar to those under which the fruits were acted upon by the wind. The almost complete absence of friction and the accuracy of the instrument are both proved by the fact that in a wind sufficient to balance the weight of the scale pan and thread the placing of a weight of .01 gms. on the scale pan brings the beam as far out of the vertical as the construction of the stand will allow. An accuracy of .001 gms. is certainly not too much to claim for the instrument.

The smallest weight which it is possible to use is .16 gms., this being the weight of the scale pan and its suspending thread.

Structure and Properties of the Wind Used.

The strength of the wind produced by the fan varied with the four speeds as above mentioned, and the strength of the wind entering the tube could be controlled further by moving the tube away from or towards the fan. The tube was kept carefully aligned with the centre of the fan.

Smoke was passed through the tube and no marked rotatory movement was observed; the smoke passed straight through, never twisting through an angle of more than 90°. Close to the inside surface of the tube it was retarded and continued to come out for some time after the central mass had passed. The region of retardation was very narrow compared with the width of the tube. It is clear, therefore, that the wind is more or less horizontal with a straight movement through the tube.

The structure of the wind was further investigated by means

of the anemometer, and it was found that there was a hollow cone of relative calm near the centre of the fan with Speed 4; this cone extended about 10-15 cms. from the boss of the fan. Beyond 20 cms. the wind had a steady horizontal pressure, and with lower speeds no cone of calm could be detected.

It was further found that the pressure of wind in the tube at the end furthest from the fan was practically the same as the pressure obtained without the tube and with the anemometer 130 cms. nearer the fan.

As it was not possible to measure all the variations of pressure obtained the relation of the pressure of the wind to the distance from the fan was examined. A series of measurements of the pressure with the tube at various distances from the fan showed that within the limits of the experiments the pressure of the wind, except for Speed 4, varied approximately inversely as the distance of the near end of the tube from the fan. The measurements and ratios are given in Table IX. It is possible, therefore, to calculate from a few measurements the pressure at any given distance.

TABLE IX.

Speeds of Fan.	Distance of Tube	Pressure on Disc as measured.	Ratios
Speed 1.	26.5 cms.	.18 gms.	1.0 : 1.125
"	30.5 "	.16 "	1.150 : 1.0
Speed 2.	29.5 cms,	.36 gms.	1.0 : 2.25
"	44.5 "	.26 "	1.5 : 1.6
"	75.5 "	.16 "	2.5 : 1.0
Speed 3.	26.5 cms.	.56 gms.	1.0 : 3.5
"	40.5 "	.36 "	1.5 : 2.25
"	63.5 "	.26 "	2.4 : 1.6
"	103.5 "	.16 "	3.9 : 1.0
Speed 4.	28.5 cms.	.50 gms.	1.0 : 3.1
"	87.5 "	.25 "	3.0 : 1.6
"	144.5 "	.16 "	5.0 : 1.0

Since within the limits of the experiments $P=kV$, where P is the pressure, V the velocity and k a constant, $V=\frac{P}{k}$. The constant k in these experiments is taken as .0025 gms., which is the pressure on one sq. cm. of a wind with a velocity of one m.p.h.¹

¹ This is calculated from the constant given by Berget (4), velocity of 1 metre per second=pressure of 125 gms per sq. metre. This figure is also approximately the same as the theoretical pressure calculated from the density of the air.

In this way the velocity of the wind used in each experiment can be calculated from the pressure such a wind has upon the disc of the anemometer.

Constants—

Diameter of Tube=4.5 cms.

Length of Tube for Dispersal=125 cms.

Area of Disc of Anemometer=8.55 sq. cms.

$k=.0025$ gms.

Method.

The essence of the experiments lies in dropping the fruits through the hole D in the tube and determining the maximum amount of wind which has no effect on the fruit when it has once fallen, and also the minimum amount of wind which blows the fruit right through the tube. Preliminary experiments showed that the relative humidity of the air had an effect on the results, so that the R.H. was determined at the time of each set of observations. As the general phenomena are very similar for each species one example will now be given in detail.

Taraxacum officinale, Weber.—The same fruit, an average one, was used throughout the experiment. It was manipulated with tweezers and inserted through the hole into the tube. Two or three observations were taken with the tube at each of the several distances from the fan, the distance being measured from the heavy end of the fruit in each case. The results are given in Table X. The Relative Humidity was .77; the pappus spread out to form a flat disc-like surface by means of a pulvinus of the *Lactuca* type (see Chap. V, A). The lowest speed of the fan was used throughout the experiment.

In Table X the first column gives the distance from the fan of the near end of the tube. From these measurements the pressure on the disc is calculated from the observed pressure of .16 gms. at 30.5 cms. (cp. Table IX); this pressure is given in gms. per sq. cm. in the third column. The velocities calculated from the observed pressure, taking $k=.0025$ gms. in the formula $V=\frac{P}{k}$, are given in the fourth column. These figures are calculated to the second decimal place, but under the conditions of the experiment the accuracy of the results is scarcely of that degree. The main point is that they are very much less than would be the case if the mechanics were simply those of a body falling in quiet air.

TABLE X.

Distance of tube from fan.	Distance fruit was blown.	Pressure on disc in gms. per sq. cm.	Velocity equivalent in m.p.h.
13.5 cms.	out immediately.	.0422	4.11
23.5 "	" "	.0242	3.11
33.5 "	" "	.0168	2.59
43.5 "	" "	.0132	2.29
53.5 "	" "	.0107*	2.06
63.5 "	out, touched.	.0090	1.84
73.5 "	" "	.0078	1.76
83.5 "	" "	.0068	1.64
93.5 "	out slowly.	.0061	1.56
103.5 "	out, more slowly.	.0055	1.48
113.5 "	39.72 cms.	.0051	1.42
123.5 "	24.30 "	.0016	1.35
133.5 "	18.30 "	.0043	1.31
143.5 "	17.22 "	.0040	1.26
153.5 "	15.18 "	.0037	1.21
163.5 "	11.13 "	.0035	1.18
173.5 "	9.14 "	.0033	1.14
183.5 "	5.7 "	.0031	1.11
193.5 "	5.9 "	.0029	1.07
203.5 "	4.6 "	.0028	1.05
213.5 "	3.4 "	.0026*	1.01
223.5 "	2.3 "	.0025	1.00
233.5 "	2.4 "	.0024	.98
243.5 "	0.4 "	.0023	.95
253.5 "	0.3 "	.0022	.93
263.5 "	1.3 "	.0021	.91

Table X. Observations on Fruit Dispersal of TARAXACUM OFFICINALE. For explanation see text.

Between the point at which the fruit was blown through the tube with no stop whatever and the point at which the fruit was not moved when once it had fallen there was an interesting transition region from 63.5 cms. to 173.5 cms. in which the fruit was blown along in jumps.

Up to 53.5 cms. the fruit was blown straight through, and as far as could be seen did not touch the tube at all. From 63.5 cms. to 103.5 cms. the fruit was blown along trailing with its tip just touching the tube or in a few long jumps. There was sometimes a distinct interval between the jumps, during which the fruit remained lying quite still or showed only feeble signs of movement. This period of rest indicates slight changes in the pressure of the wind, but these were so slight that they are for the present negligible.

The time taken by the fruit to reach the end of the tube increased considerably from 93.5 cm. to 103.5 cms., and after that only five minutes were allowed to elapse between inserting the

fruit and taking the reading. From 113·5 cms. to 173·5 cms. the jumps decreased in length, and after 213·5 cms. the fruit lay where it fell with no further movement.

As the rate of fall in quiet air is about 1 m.p.h. and the wind after 173·5 cms. is about 1 m.p.h. the fruit would be carried a distance equal to that of the fall, if the wind had no other effect than that claimed by Praeger. The diameter of the tube is 4·5 cms. and the length of the fruit about 1 cm., so that the distance of the fall is about 3·5 cms. It will be noticed in Table X that 203·5 cms. is the last point at which the fruit is carried to a distance which is greater than the diameter of the tube. The next reading gives a distance of 3·4 cms., and at this point it can be assumed that the fruit falls as it would in quiet air. There is considerable irregularity in the readings when the wind falls below 1·2 m.p.h. and all that is claimed as really accurate is that a wind of more than 1·01 m.p.h. blows the fruit further than it would do if it had only the effect of mass transport at the speed of the wind as suggested by previous investigators. Below 1·01 m.p.h. the distance travelled by the fruit varied from 0 to 4 cms.

The two points to which particular attention has been paid are:—

1. The least wind-pressure necessary to blow the fruits right through the tube with no stop and without the fruit touching the tube in any way; this is referred to as the critical pressure A.

2. The highest wind-pressure which could be used without moving the fruit once it had fallen; this is referred to as the critical pressure B.

These two points are marked in Table X at ·0107 gms. per sq. cm. and ·0026 gms. per sq. cm., and their significance is discussed in Section C. Other fruits are examined more or less in the same way, and the results are summarised below.

Senecio vulgaris, L. Material collected in the open; the R.H. was ·77.

Critical Pressure A—·0055 gms. per sq. cm. 1·48 m.p.h.

Critical Pressure B—·0035 „ „ 1·18 „

Senecio vulgaris, L., var. *radiatus erectus*, Trow.—Authentic material for which I am indebted to Professor A. H. Trow. It was found that whereas the pappus remained expanded in the air after being dried in a warm tube with the R.H. as high as ·75, it closed at once when taken out of the tube with the R.H. ·80. Several

fruits were used, and it was found that between .66 and .73 the relative humidity had no effect on the wind-pressure required.

Critical Pressure A—.0078 gms. per sq. cm. 1.76 m.p.h.

Critical Pressure B—.0046 „ „ 1.35 „

It will be noticed that in both cases the figures are higher than those for the previous material. The fruits were plumper in the variety, but the pappus had about the same development in each. The pulvinus in these two cases is the *Lactuca* type; the pappus hairs are setose-scabrid as in the dandelion, but the pappus is sessile, not stipitate as in the latter fruit, and spreads at an angle of about 45° with the axis of the fruit, not at right angles to give a flat surface as in *Taraxacum*.

Tussilago Farfara, L.—This was taken as an example of the simple setose pappus with a *Tussilago* type of spreading (see Chap. V, A). As most of the 'fruits' are sterile with empty pericarps care was taken to choose mature fertile fruits, which were obtained in the open. The pappus was too large for the hole in the tube, so the fruit was inserted to a distance of 6 cm. before being liberated. With the R.H. .78 or below drying was unnecessary as the pappus expanded spontaneously under these conditions.

Critical Pressure A—.00087 gms. per sq. cm. .59 m.p.h.,

Critical Pressure B—.00081 „ „ .57 „

It will be noted that the two critical points are very close together. The behaviour of the coltsfoot fruit was peculiar. So slight is the wind necessary for its dispersal that persons walking along the room made sufficient wind to blow the fruit right through the tube. Special care was taken, therefore, to carry on the experiment on a still day with no one moving in the room at the time of the reading,

It was found that with the fan at the lowest speed, and the tube 658.5 cms. away, the fruit was blown right through the tube sometimes with, sometimes without, pauses. At a distance of 703.5 cms. the fruit remained motionless for about five minutes and then moved a distance of 5–40 cms. The critical pressure B is therefore too high, but it was not possible at the time to carry the experiment further, as a complete absence of external currents of air is necessary for the accurate determination of the constant in this case.

Centaurea imperialis, Hausskn.—This was taken as an example of a heavy fruit with a pappus of numerous paleaceous setæ. The spreading of the pappus is accomplished by means of a pulvinus to each seta, the *Cirsium* type of Taliew (see Chap. V, A). As

mentioned previously (Chap. V, A) the pappus is sensitive to a difference of .03 in the R.H., opening spontaneously at R.H. .75 and closing at R.H. .78 when opened by artificial drying. The third speed of the fan was used.

Critical Pressure A—.1318 gms. per sq. cm. 7.2 m.p.h.

Critical Pressure B—.0232 „ „ 3.0 „

Ursinia speciosa, D.C.—This was taken as an example of a fruit with a distinctly paleaceous pappus. The fruit has a small tuft of hairs at the base and five, well developed, white and gold plumoso-paleaceous scales at the top. The fruit is not particularly heavy, but the pappus is relatively solid, and its weight is somewhat of the same magnitude as that of the fruit itself, not, as in the other cases, very much smaller than that of the whole structure. The spreading of the pappus seems to be more or less permanent in this case, and no pulvinus could be detected. The third speed of the fan was used.

Critical Pressure A—.0514 gms. per sq. cm. 4.5 m.p.h.

Critical Pressure B—.0118 „ „ 2.1 „

Leontopodium alpinum, Cass.—The fruit in this case is small and more or less spherical with no pappus. The average diameter of the fruit is about .25 mm. The small size of the fruit prevented accurate measurements with the apparatus as arranged. With the tube at 33.5 cms. and the fan at Speed 4 six fruits were dropped through the hole. This was repeated three times with the result that about half the fruits were blown right through the tube, and the others were blown a distance which varied from 35 cms. to 90 cms. The critical pressure A is, therefore, about .050 gms. per sq. cm., equivalent to 4.4 m.p.h. Six fruits were dropped through the hole with the tube at 33.5 cms. and the fan at Speed 1. Three of them were blown about 5 cms. and the others were lost. The critical pressure B is, therefore, not more than .0168 gms. per sq. cm., equivalent to not more than 2.59 m.p.h.

C. HYDRODYNAMICS OF WIND-DISPERSAL.

According to the views of Dingler and Praeger the dandelion fruit, which falls in quiet air at the rate of .98 m.p.h., would require an uniform wind of about 50 m.p.h. and an initial elevation of about one mile in order to be transported about 50 miles, or 1 cm. elevation for 50 cms. dispersal. In other words the ratio $\frac{\text{distance travelled}}{\text{initial elevation}}$ is a measure of the velocity of the wind required.

In the apparatus described above the initial elevation is at most 4.5 cms. (the diameter of the tube) and the maximum distance travelled can be taken as the length of the tube, 125 cms. The wind-velocity necessary for the transport of the dandelion fruit to the end of the tube would then be $\frac{125}{4.5}=28$ m.p.h. approx. The experimental result, as shown in Section B, is 2.06 m.p.h. approx. This discrepancy requires some explanation and the essential point lies in the fact that the wind-dispersal of pappose fruits has been regarded hitherto as a hydrostatic problem and not as the hydrodynamic problem which it undoubtedly is. The average pappose fruit is more akin to an aeroplane or a kite than to a parachute or balloon. An aeroplane has a much greater rate of fall in quiet air than a dandelion fruit but a wind of 60 m.p.h. is sufficient to keep the former in the air indefinitely. It must also be noted that as long as the "air speed" is 60 m.p.h. an aeroplane remains up, so that in a wind of 90 m.p.h. an aeroplane could actually drift backwards at the rate of 30 m.p.h. in relation to the earth. This case is somewhat similar to that of the pappose fruit (see below); there would be a considerable element of danger in the above-mentioned stunt but I am assured by aeronauts that it is possible.

Hydrodynamics of Fruit-Dispersal in

TARAXACUM OFFICINALE.

The dandelion fruit is taken as the simplest example. Here the main weight of the fruit is at the base of the slender stalk, while at the top of the stalk there are the numerous hairs of the pappus which spread out when the R.H. of the air is .77 or less. These hairs form a flat, circular surface at right angles to the main axis of the fruit; the centre of gravity is low, so far the structure is that of a simple parachute and is relatively stable.

Now if the fruit is considered to be vertical at first (Fig. 27, A) and a wind with a velocity which develops a pressure M impinges on the fruit in such a position, the pappus being lighter than the heavy fruit body, the fruit does not remain erect. The pappus is acted upon more strongly and is blown ahead of the fruit body, so that the whole fruit becomes tilted as in Fig. 27, B. Once this position is reached the force M can be resolved into two components S and R , S being parallel with the surface of the pappus and R at right angles to that surface. The two components are equal to $M \sin \theta$ and $M \cos \theta$ respectively, θ being the angle of the

axis of the fruit with the horizontal (see Fig. 27, B). The tangential component S is known in kite dynamics as surface slip and is usually considered negligible.

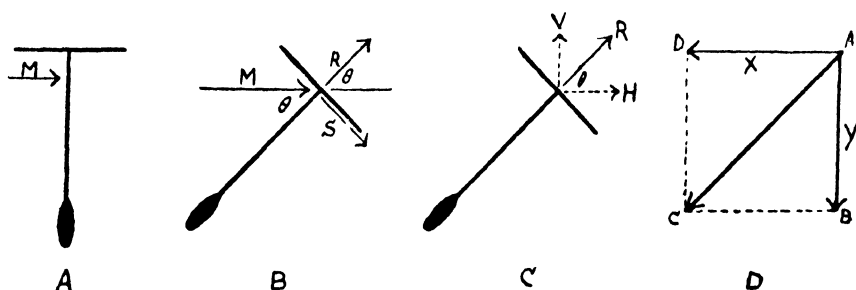


FIG. 27. Resolution of Forces (for explanation see text).

The Vertical Component.—The normal component R can be resolved further into two components (Fig. 27, C) a vertical component V and a horizontal component H . The vertical component V is equal to $R \sin \theta$ and the horizontal component H to $R \cos \theta$. Since $R = M \cos \theta$, $R \sin \theta = M \cos \theta \sin \theta$, therefore $V = M \cos \theta \sin \theta$. If the pappus surface were a continuous membrane or acted as a continuous membrane (of the area occupied by the hairs and the interspaces) and if the wind were just sufficient to keep the movement of the fruit horizontal the vertical component would be equal to the mass of the fruit. As the pappus is not a continuous membrane the minimum pressure on the area of the circle of the pappus surface may be greater than the weight of the fruit. This minimum pressure is described below as the critical vertical component, which is of course a pressure, not a velocity.

The Horizontal Component. The horizontal component is equal to $R \cos \theta$, which is equal to $M (\cos \theta)^2$.

Surface Slip. The component S can be resolved into a horizontal and a downward vertical component. These will be equal to $x S \sin \theta$ and $x S \cos \theta$ respectively; where x is a small fraction. The close similarity of the experimental and the calculated results (see Table XI) shows, that x is so small that S can be neglected.

Data.

For any further consideration various data are necessary and these have been obtained.

Weight of the Fruit. Bessey (5) gives .00044 gms as the weight of the dandelion fruit but it was considered necessary to determine the weight of the fruits actually used. One hundred whole fruits were weighed carefully.

Wt. of 100 fruits= $\cdot 0756$ gms.

\therefore average weight of one fruit= $\cdot 000756$ gms.

This is of the same magnitude as Bessey's figure and the difference is possibly due to the fact that the fruits used were very well developed.

Area of Pappus Surface. The constant referred to by this name is not the sum of the areas of the exposed surfaces of the hairs as calculated by Dandeno (9) but the area covered by a circle with a diameter equal to twice the length of a pappus hair. The pappus from eight fruits was stuck to paper and measured under a dissecting microscope. The longest hairs and the mass of hairs were both measured.

Diameter in mm. as measured by the longest pappus hairs= $12\cdot 5, 12\cdot 0, 12\cdot 0, 12\cdot 0, 12\cdot 0, 12\cdot 5, 12\cdot 0, 12\cdot 0$. Average= $12\cdot 12$ mm.

Diameter in mm. as measured by most pappus hairs= $12\cdot 0, 11\cdot 5, 11\cdot 5, 11\cdot 5, 11\cdot 5, 12\cdot 0, 11\cdot 5, 11\cdot 5$. Average= $11\cdot 62$ mm.

As the efficiency of the pappus would seem to depend on the surface formed by the mass of pappus hairs rather than upon the few longer hairs, $11\cdot 62$ mm. was taken as the average diameter of the pappus surface. The average area of the pappus surface, therefore, is $1\cdot 06$ sq. cm.

Angle of the Axis. As the fruit was in movement during dispersal observations were not accurate. The angle of the axis with the horizontal appeared to vary between 45° and 60° . Photographic measurement should be possible and will be used in subsequent experiments.

Rate of Fall in Quiet Air. The determination of this constant by Praeger (30) is taken as sufficiently accurate and is converted into m.p.h.; 12 feet in 8.5 seconds= $\cdot 98$ m.p.h.¹

The Vertical Component. In the experiments described in Section B the wind was always lateral, so that a wind with the minimum or critical vertical component also had a horizontal component. Any wind-pressure which lifted the fruit when it had once fallen was, therefore, due to a wind, the total force of which exceeded the critical vertical component. This component is taken to be the pressure of the maximum wind which does not blow the fruit more than 4 cm. (see below under Winds between "W" and "V"). The chief source of error in the experiment is the friction

¹ This is calculated from the rate of fall (12 feet in 8.5 seconds) recorded by Praeger. He gives inversion of the time and multiplication by 8 as a method for approximating in m.p.h. the observed rates of fall in secs. per 12 feet. A closer approximation is obtained by using 8.4 instead of 8 and this has been used in the present calculations.

between the glass and the fruit, but in the case of the dandelion the fruit rests on the glass on the tips on a few pappus hairs and a very small portion of the surface of the fruit body. Friction in such a case is reduced to a minimum. Another possible source of error is the adhesion of the fruit to the glass; this might arise from a mucilaginous pericarp or from mucilaginous achenial hairs, both of which are absent in the dandelion, so that this source of error is eliminated. A third possible source of error is the assumption that the effect of the tangential component *S* is negligible but this assumption is justified by subsequent observation and calculations.

With the dandelion the observed maximum wind which does not move the fruit is 1.01 m.p.h. (see table X) and in this case it can be taken as the velocity of wind with a pressure equal to the critical vertical component, .0026 gms. per sq. cm.

Theoretical Conclusions.

From these observed data various conclusions can be drawn, and the more interesting points will now be considered.

Fall in Quiet Air. The first interesting point arises from the close similarity between the rate of fall in quiet air, .98 m.p.h. and the experimental value found for the critical vertical component, which is equivalent to 1.01 m.p.h. This is easily explained from the hydrodynamical point of view. In still air there is no lateral force, therefore there is no tilting of the fruit. The pappus surface is horizontal, so that there are two forces acting during the fall, the mass of the fruit and the pressure exerted by the air impinging on the pappus with a velocity equal to the rate of fall. The latter force is similar to that acting with a lateral wind but in this case it all acts in a vertical upward direction. The mass of the fruit acts downwards in a vertical direction.

The fruit in quiet air rapidly acquires the terminal velocity of fall, then the upward force is equal to the downward force, the fall being due to the momentum gained before the terminal velocity is reached. The upward force due to a fall at the rate of .98 m.p.h. is equivalent to a wind with a velocity of .98 m.p.h. The experimental value, 1.01 m.p.h., found is quite a close approximation, especially when it is remembered that, as Praeger mentions, there is some variation in fruits collected from different heads, although those from the same head are very similar. The rate of fall in quiet air is at least approximately equal to the velocity of the critical vertical component and is more easily and accurately measured by

the method of Dingler and Praeger than by the rather tedious method adopted in the present investigation.

The Critical Vertical Component. Although the pressure and the velocity equivalent to the pressure of the critical vertical component can be calculated as shown in Section B) from the known pressure of the maximum wind which does not move the fruit, the actual value of the pressure on the pappus can be determined only when the area of the pappus is known. This constant as shown above is 1.06 sq. cms., therefore the pressure of the critical vertical component on the area of the pappus is $\cdot 0026 \times 1.06 = \cdot 002756$ gms.

The Efficiency of the Pappus. If the pappus acted as a continuous membrane the total pressure of the critical vertical component would be equal to the weight of the fruit, but the hairs of the pappus do not form a continuous membrane. Some of the wind passes between the hairs and exerts no effective pressure. The pressure actually exerted on the pappus by the critical vertical component, is, of course, equal to the weight of the fruit, so that the fraction $\frac{\text{pressure actually exerted on the pappus}}{\text{pressure of } V \text{ on the area of the pappus}}$ gives the efficiency of the pappus as a sail or wind-holding mechanism. This efficiency is, therefore, $\frac{\cdot 000756}{\cdot 002756} = \cdot 27$.

The Minimum Wind for Dispersal. In discussing the resolution of the pressure in Fig. 27 the fruit was regarded as stationary, but it is in motion during dispersal. The point of view upheld by previous investigators is that the fruit rapidly attains the velocity of the wind which is dispersing it. A little consideration of the diagrams in Fig. 27 will make it quite clear that H, the horizontal component, is considerably less than M, the total pressure, when the fruit is at an angle of 45°. If the fruit were vertical, H would be eliminated and the mechanism would act only as a balloon. On the other hand if the fruit were almost horizontal (*i.e.* the pappus almost vertical) V would be small compared with H. Even in the latter extreme case, however, although H would be almost equal to M, the efficiency of the pappus being only $\cdot 27$, the horizontal component H would have only the effect of $M \times \cdot 27$. It is clear then that, even when H attains its maximum value, the velocity at which the fruit would be blown would be less than the velocity of M and therefore the fruit would never attain the velocity of the wind.

From the preceding data it is possible to calculate the minimum wind required for dispersal of the fruit to a distance which

is limited only by the presence of obstacles such as trees and mountains, and by the relative humidity of the atmosphere.

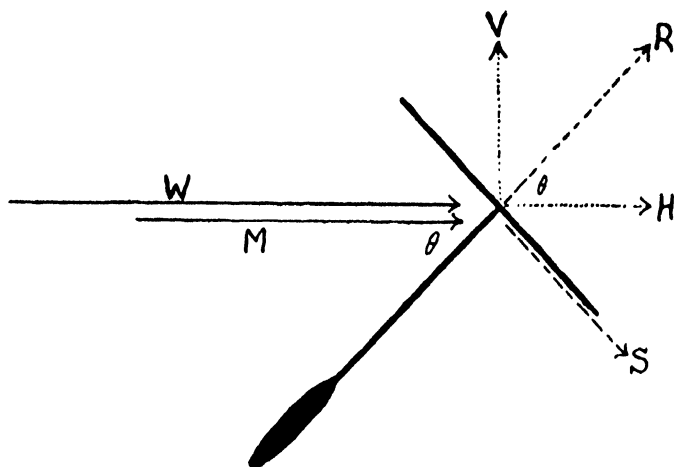


FIG. 28. For explanation see text.

Considering Fig. 28, let

W = pressure of the minimum wind for dispersal,

w = velocity equivalent to W ,

M = pressure of the effective part of W ,

m = velocity equivalent to M , *i.e.*, the rate at which the wind overtakes the fruit moving with the velocity of h .

R = normal component of M ,

S = tangential component of M (*i.e.*, surface slip),

H = horizontal component of R ,

H' = pressure exerted on the pappus by H ,

h' = velocity equivalent to H' ,

V = vertical component of R ,

θ = angle of axis of fruit with horizontal.

Since the value of V is $M \cos \theta \sin \theta$, the minimum wind required for dispersal will depend on the value of $\cos \theta \times \sin \theta$ and thus on the angle at which the fruit is tilted. The product of $\cos \theta \times \sin \theta$ varies from $+ \cdot 5$ to $- \cdot 5$ and reaches its maximum value of $+ \cdot 5$ when $\theta = 45^\circ$. The position of the fruit in which $M \cos \theta \sin \theta$ reaches its maximum value for any given wind is, therefore, with the axis of the fruit at 45° to the horizontal. Since any wind which is able to lift the fruit will carry it along, the minimum wind which will disperse the fruit will be the one with which the fruit assumes an angle of 45° . The value of θ in this particular case is, therefore, 45° . An angle of 45° for the pappus (with the fruit in the normal position) is the usual one for the pappus in the

Compositæ, another example of the efficiency in detail which is characteristic of the family.

$$\text{With } \theta=45^\circ, V=M \cos \theta \sin \theta=.5 M$$

$$H=M(\cos \theta)^2=.5 M$$

$$\therefore H=V \text{ and } M=2 V$$

the value of V as determined experimentally is .0026 gms. per sq. cm.

$$\therefore H=.0026 \text{ gms. per sq. cm. and } M=.0052 \text{ gms. per sq. cm.}$$

The efficiency of the pappus as calculated from the known value of V for the area of the pappus and from the weight of the fruit is .27.

$$\therefore H'=.0026 \times .27=.0007 \text{ gms. per sq. cm.}$$

The pressure M depends on the velocity with which the wind overtakes the fruit as it moves along and the velocity of the effective part of the wind is the difference between the velocity of the wind and the velocity of the fruit, *i.e.* $m=w-h'$ ($\therefore w=m+h'$).

The pressure M (.0052 gms. per sq. cm.) is equivalent to a velocity of 1.44 m.p.h., *i.e.*, $m=1.44$ m.p.h.; the pressure H' (.0007 gms. per sq. cm.) is equivalent to a velocity of .53 m.p.h., *i.e.*, $h'=.53$ m.p.h., but $w=m+h'$, $\therefore w=1.44+.53=1.97$ m.p.h.

In this way we find that the minimum wind for dispersal has a velocity of 1.97 m.p.h., which is equivalent to a pressure of .0097 gms per sq. cm. Referring to Table X we find the critical pressure A is .0107 gms. per sq. cm., which is equivalent to 2.06 m.p.h. At the next point taken in the experiment the velocity had fallen to 1.84 m.p.h.: the fruit skimmed along the tube, touching it with the base only, being thus partially supported and leaving the wind free to exert a pressure sufficient to blow the fruit right out of the tube. The critical pressure A in the case of *Taraxacum officinale* is clearly an approximation to the pressure of the minimum wind required for dispersal. Whether it is so for other species remains to be determined.

In the case of the dandelion we thus arrive at the interesting conclusion that the critical pressure A is approximately equal to W , the pressure exerted by the minimum wind necessary for dispersal, and that the critical pressure B is approximately equal to V , the pressure of the minimum vertical wind which will support the fruit *i.e.*, the pressure of the minimum or critical vertical component of the effective part M of the horizontal wind W . In the language of aeronautics 1.44 m.p.h. is the minimum air speed of the dandelion fruit; the difference in the two cases is that so long as the aeroplane

overtakes the wind at not less than 60 m.p.h. it stays up, and so long as the wind overtakes the fruit at not less than 1.44 m.p.h. the fruit stays up.

Winds between "W" and "V."—If the wind exerts a pressure of .0107 gms. per sq. cm. the fruit is blown right through the tube without touching, and if the wind exerts a pressure of .0026 gms. per sq., cm. or less, the fruit does not move once it has fallen. Between these two points the fruit moves but touches the tube, and it is of interest to follow the action of the wind with pressures between W and V.

In the initial stages of flight the wind exerts its full pressure, *i.e.*, $M=W$, but as soon as it has developed an effective action the fruit moves and M becomes less than W . Since the continued flight depends on V being not less than the critical value the fruit will fall: thus if $W=.0052$ gms. per sq. cm. M will be less than that and V will be less than .0026 per sq. cm., which is the minimum vertical component which keeps the fruit up; the fruit will therefore fall. When reference is made to Table X it will be noted that if W is greater than .0052 gms. per sq. cm. the fruit moves along continuously but is partly supported by the tube. It is only when W falls below the minimum value of M that the fruit actually stops.

If W is less than .0052 gms. per sq. cm, then V can never, even in the initial stage, be as much as .0026 gms. per sq. cm., so that the fruit must fall; but the time taken to fall will depend on the upward pressure exerted by the vertical component. The fruit will fall slowly if V is nearly .0026 gms. per sq. cm., and more quickly the smaller the value of V becomes.

The value of V depends on the value of W and on the value of θ . The product $\cos\theta \times \sin\theta$ diminishes gradually until when the fruit is vertical it is nothing. The smaller W becomes the greater θ becomes, because the pappus is not blown so much before the fruit body, so that the smaller W becomes the smaller becomes $\cos\theta \times \sin\theta$, and therefore V becomes smaller very rapidly.

As soon as W is equal to the rate of fall in quiet air the axis of the fruit becomes vertical; then there is no vertical component of W and the fruit falls with a velocity equal to that of the wind. The initial elevation is then equal to the distance travelled by the fruit. This may be made clear by considering the parallelogram of forces in Fig. 27, D. The force X is equal to the force Y , and they act at right angles to each other, the resultant is AC , which is the path of fall of the fruit. It is then clear that $AB=BC$,

i.e., the distance travelled by the fruit is equal to the initial elevation. The force *X* is different from the pressure *M* or *W* in that the fruit is being carried along as a balloon is carried along with a velocity equal to the velocity of the wind.

From the above it is clear that what is really measured in the experiments on the critical pressure *B* described in Section B is not the minimum vertical component of *M* but the rate of fall, which is, however, equal to the latter constant. It would be possible to measure the critical vertical component directly with a modified apparatus, and the writer hopes to continue the investigation.

The conclusion to be drawn from the experimental and theoretical treatment of the hydrodynamics of the dispersal of the dandelion fruit may be stated briefly thus—so long as the relative humidity of the air remains above .77 and so long as the fruit does not encounter an obstacle, a horizontal wind of 1.97 m.p.h. is sufficient for its dispersal to any distance.

If the air becomes moist the pappus closes up and the fruit falls rapidly. The problem of surmounting low obstacles is partly solved by the elongation of the scape, which takes place during the twenty-four hours before the fruits are ready for dispersal. The scape elongates 50% to 90% of its original length, *e.g.*, from 24 cms. to 38 cms. and from 20 cms. to 38 cms. in cases which were measured. This sudden elongation is due to a stretching of only the upper part of the scape: the stretching causes the elongated part to be paler in colour since the chlorophyll is not increased in proportion to the increase in surface. The physiology of the phenomenon seems to be somewhat as follows—during the ripening of the fruits there is a marked streaming of carbohydrates up the scape to the capitulum. This streaming does not cease immediately on the maturation of the fruits, and the materials accumulate in the upper part of the scape. This causes the osmotic pressure and the turgidity of the cells in that region to increase so much that the cell walls are stretched along the line of least resistance, *i.e.*, longitudinally. Accurate experiments are, however, necessary to prove this conclusively, and the point appears to be of general interest in view of the similar quick elongation of the supporting stalk in the spore-dispersal of many Bryophyta, and the similar but slow elongation in the peduncles during the fruiting stage of many Angiosperms. Beeby (3) observed similar elongation in the scape of *T. spectabile*, var *maculiferum*, but was "not able to give exact details concerning the times at which

elongation takes place." Cassini (8) had previously recorded the phenomenon in *Tussilago Farfara* and *Chevreulia stolonifera* but gave no details.

The Hydrodynamics of Fruit-Dispersal in other Species.

The theory of the experiments with the other fruits is complicated by the angle at which the pappus spreads in *Senecio*, *Ursinia* and *Centaurea*, by the presence of mucilaginous achenial hairs in *Senecio*, the presence of a basal tuft of hairs in *Ursinia* and the absence of a pappus in *Leontopodium*. The structure is in no case that of a simple parachute with the wind-holding surface at right angles to the axis of the fruit, as in *Taraxacum*.

Senecio vulgaris, L.—According to Praeger the fruit of *Senecio vulgaris* falls in quiet air at the rate of 12 feet in 12·8 seconds, which is approximately ·66 m.p.h. This is considerably lower than the value (1·18 m.p.h.) obtained for the velocity equivalent to the critical pressure B in this species. There are several sources of inaccuracy, but if ·66 m.p.h. is taken as the velocity of the critical vertical component, it is possible to make a rough calculation of the minimum wind for dispersal. The efficiency of the pappus can be taken as approximately ·25 and calculating as in the case of *Taraxacum*,¹ the minimum wind for dispersal is 1·25 m.p.h. This is quite a good approximation to the value (1·48 m.p.h.) found for the velocity equivalent to the critical pressure A in the experiments described above.

Centaurea imperialis, Hausskn.—As Praeger does not give the rate of fall in this species an approximate measurement of this constant was made by his method and the value found was 2·2 seconds for a fall of 12 feet. This is equivalent to 3·81 m.p.h. Calculating as before we get 7·3 m.p.h. as the minimum wind for dispersal. These two values (7·3 and 3·81) are sufficiently near the experimental values (7·2 and 3·0) found for the velocities equivalent to the critical pressures A and B to show that the methods of experiment and calculation are both approximations to the actual values of the two constants.

Ursinia speciosa, DC.—The rate of fall was determined in this case also for the purpose of this calculation. The value found was 3·4 seconds for a fall of 12 feet. This is equivalent to 2·47 m.p.h. Calculating as before we get 4·7 m.p.h. as the minimum wind for dispersal. These two values (4·7 and 2·47) are quite good

¹ The tilting of the fruit need not occur in this case as the pappus is already at an angle with the horizontal. The formula for the calculation is $w = \sqrt{\frac{1}{2}F^2} + \sqrt{2F^2}$ where F is the rate of fall in m.p.h.

approximations to the experimental values (4.5 and 2.1) obtained for the velocities equivalent to the critical pressures A and B. The minimum wind for dispersal in these three species is clearly approximately the same as the minimum wind required to blow the fruits out of the tube without a pause. It is also closely approximate to the value calculated from the rate of fall assuming the angle to be 45° and the efficiency of the pappus to be .25. We have, therefore, a convenient although somewhat rough method for the calculation of the minimum wind required for the dispersal of those pappose fruits of which the rate of fall in quiet air is known.

Leontopodium alpinum, Cass.—These fruits not being pappose the preceding methods do not apply, and as they are spherical the dispersal is more analogous to spore dispersal or to the cases given by Thoulet (35) and Udden (37), see section D. Considering the very slow winds which are sufficient for the dispersal of spores it is probable that the velocity (4.4 m.p.h.) equivalent to the critical pressure A is at least an approximation to the minimum wind for dispersal in this species. It is interesting to note that, although Stokes' Law may apply in this case, the cypsela in the Compositae when epappose is usually cylindrical. It has been shown by Eiffel (13) that a cylinder has a much slower rate of fall than a sphere of the same diameter, for instance, if the length of a cylinder is equal to the diameter and the movement is in the direction of the axis, the resistance of the air is five times greater than it is for a sphere of the same diameter moving at the same rate.

D. PHYLOGENETIC SIGNIFICANCE OF FRUIT-DISPERSAL.

The significance of the hydrodynamics of fruit dispersal may not be immediately obvious, but the question of whether a given fruit requires for its dispersal a wind of 2 m.p.h. or a wind 50 m.p.h. is of fundamental importance in the interpretation of the facts of geographical distribution. A proper understanding of the conditions of wind-dispersal is necessary for the rational study of the history of the Compositae, their migrations and colonisations, their paths of travel and regions of concentration, which form the subject of the following chapter.

De Candolle (11), who is followed by Bentham (1, 7), Praeger (30), Willis (IV, 94) and others, ignores or gives rather unsubstantial reasons for neglecting the authentic evidence for wide dispersal, and gives a series of negative observations in support of the dispersal for short distances only. That such generalisations from particular

observations are not sound is amply proved by the cases recorded by Treub (36), Penzig (29), Ernst (15), Gates (19), Vogler (38-40) and others (see Sect. A), and the argument given by Wallace makes it clear that negative evidence in this matter has very little value. Further evidence of the transporting power of wind is given by Udden (37), who showed that particles between .001 mm. and .04mm. are apparently completely borne up by a wind of 8 m.p.h. Thoulet (35) states that a hailstone 5 mm. in diameter could be sustained in the air by a wind of about 22 m.p.h. and one of 10 mm. diameter by a wind of about 33 m.p.h. After summing up the available evidence on the dispersal of dust particles Evans (16) says, "In any case, it is sufficiently demonstrated that particles of detritus up to about 100 microns in diameter, . . . , are capable of remaining suspended in moving air for an indefinite period. A very moderate wind will carry them along with it, and a slight unevenness of the surface is sufficient to give rise to an upward current of the air, which will raise its freight of minute mineral particles high above the ground."

Since dust particles of the size mentioned have a rate of fall which is two to four times that of the average papoose fruit, it is not unreasonable to suppose that moving air will have an effect on such fruits equal to its supporting effect on more or less spherical particles which are not so well adapted for dispersal by wind.

It has been calculated by Udden (see Evans, 16 p. 254) that in the west of the United States an average of about 850,000,000 tons of dust is carried 1,440 miles in each year. It is not unreasonable to suppose that such a weight might include some papoose fruits, which have an average buoyancy more than equal to the buoyancy of the larger particles of dust. Evans also refers to observations of particles of sand as much as .2 mm. in diameter being blown from the Sahara as far north as Hamburg. As the rate of fall of such particles is considerably greater than that of most papoose fruit this is further evidence for the probable dispersal of such fruits to considerable distances. Spherical fruits such as those of *Leontopodium alpinum* with a diameter of .25mm would be transported long distances at least as easily as grains of sand .2 mm. in diameter.

Praeger (30, p.72) also mentions that "thistle down was watched half a mile from the shore blowing seaward, and in every case its course was practically a straight line." It is quite clear that the theoretical view adopted by Praeger, that particles in moving air acquire the same velocity as the air, agrees neither with the

experimental results here given, nor with the theoretical view which enables us to calculate the minimum wind for dispersal, nor with Praeger's observation of the path of the thistle down, nor with Udden's observations on the path of solid particles in an 8 m.p.h. wind. The close accordance of the experimental velocities with the velocities as calculated from the observed rate of fall shows that the relation of the rate of fall to the velocity of the wind required for suspension of the fruit for an indefinite period is at least approximately that discussed in Section C.

The relative humidity of the air, however, has a very marked effect on the efficiency of the pappus as a dispersal mechanism, and the study of the meteorological conditions obtaining in the region of dispersal becomes necessary. In Britain, France, and Ceylon, which are the dispersal regions considered by the above mentioned opponents of long distance dispersals, wind is associated with a high relative humidity and a low relative humidity is associated with calm. The conditions necessary for long distance dispersal are a low relative humidity combined with a wind always above the minimum value of W for the particular fruit and blowing in the same direction over a large stretch of land or water. These conditions are comparatively rare in northern Europe and in Ceylon, but occur occasionally in most of the regions in which long distance dispersal has been observed.

As a result of the above investigation the writer has reached the conclusion that given these three conditions there is no limit to the distance of the dispersal of pappose fruits, and with this conclusion Dr. J. W. Evans, from his experience of the dispersal of sand, is in complete agreement. The occurrence of pappose species with a limited distribution is quite in accordance with the Law of Age and Area which will be discussed in the next chapter. The comparison by Bentham (I, 7) of the local species of *Senecio* with wide spread species of epappose genera is an example of the special pleading which has been used to explain away the obvious fact that the pappus-mechanism is an efficient means of dispersal. De Candolle's comparison by percentages of pappose and epappose species in the various tribes (11) is just as superficial. Before such comparisons (or one of wide spread pappose species with local epappose species) can be used every factor in the two cases must be balanced. These factors would include age, other means of dispersal, available habitats, the environment in which the journey starts and ends, colonising powers, physiological

differentiation, morphological differentiation during the life of the species, etc. Such a comparison has not yet been made.

The results of the present investigation which will be valuable in the subsequent study of the geographical distribution of the Compositae are (1) that the ordinary pappose fruit under the proper meteorological conditions can be blown many hundreds of miles over land or sea, (2) that hypothetical land bridges are not necessary to explain the present distribution of the Compositae, so that we can take the world as it is without raising and sinking continents, as Darwin (10) says "in a quite reckless manner." This latter is an important point as the Compositae are almost certainly of such recent origin that the possibility of land bridges is in many cases quite out of the question.

In order to facilitate reference the following summary is given of the minimum velocities of wind necessary for the dispersal of the species investigated, together with the expressions for winds of such velocities (cp. 46. p. 161)

TABLE XI.

Species.	Experimental Value in m.p.h.	Calculated Value in m.p.h.	Common Name of Wind.
<i>Taraxacum officinale</i> , Weber ...	2.06	1.97	Light Breeze.
<i>Senecio vulgaris</i> , L. ...	1.48	1.25	Light Air.
<i>Senecio vulgaris</i> , L. ...	1.76	—	Light Breeze.
var. <i>radiatus erectus</i> , Trow	.59	—	Less than a Light Air.
<i>Tussilago Farfara</i> , L. ...	7.2	7.3	Moderate Breeze
<i>Centaurea imperialis</i> , Hausskn ...	4.5	4.7	Gentle Breeze.
<i>Ursinia speciosa</i> , D.C. ...	4.4	—	Gentle Breeze.
<i>Leontopodium alpinum</i> , Cass ...			

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ERRATA.

p. 163, for $P=kV$ read $P=kV^2$.

for $V=\frac{P}{k}$ read $V=\sqrt{\frac{P}{k}}$

p. 164, for $V=\frac{P}{k}$ read $V=\sqrt{\frac{P}{k}}$

CHAPTER X.

GEOGRAPHICAL DISTRIBUTION OF THE COMPOSITÆ.

ALTHOUGH morphological characters must always be the primary data in the determination of the apparent affinities and evolutionary history of species, geographical distribution furnishes an obvious but somewhat neglected test of the truth of any deductions from structure. For instance, the Calenduleæ are practically confined to Africa and are unknown in America with the exception of one monotypic genus, *Eriachaenium*, which occurs in the Magellan region. Although this genus may be placed quite properly in the Calenduleæ from a taxonomic point of view, it is clear that its evolutionary history differs from that of the other genera in the tribe.

Up to the present point the affinities and evolutionary history of the tribes and sub-tribes have been traced only from morphological and physiological data. This chapter, which is an extension of a paper by the author (67) on the same subject, includes, in addition to the main outlines of the history of the subject, an account of the distribution of *Senecio* in some detail and of other genera, together with a discussion of these data in the light of recent developments in geographical botany and of the phyletic suggestions contained in the previous chapters.

A. HISTORY.

The most important contribution to the subject of this chapter is Bentham's elaborate exposition (I, 7), which covers the whole field from the older, purely taxonomic point of view.

General problems are dealt with by De Candolle (IX, 11), Darwin (II, 16), and Wallace (IX, 41). Don (I, 25) gives an analysis of the distribution of the Cichorieæ known at that date

(1825), while Lindley (I, 56) and Schultz Bipontinus (I, 77) treat of the subject in a somewhat perfunctory manner. The last developed his preliminary remarks in a later contribution (61). Nees (I, 67) gives a table of the distribution throughout the world of the then (1833) known genera of the Heterochrominæ. As illustrations of the new outlook on the problems of geographical distribution the papers by Andrews (3-4) and Capitaine (13) on the Leguminosæ, by Himmelbauer (39) on the Berberidaceæ and by Gates (28-29) on certain Liliaceæ may be quoted. These accounts correlate all, or at least most, of what is known about the plants with their distribution, and sound views on the evolution of the groups are more likely to result from this method than from the older method of purely morphological comparisons.

Land bridges in various parts of the world are brought in to solve many problems (cp. 74 and 82) and the Antarctic connection between Fuegia and New Zealand has been much written about (58, 66, etc.), but Hutton (42) points out that such a bridge probably did not exist after the origin of the Angiosperms, except in the form of an archipelago. In the Compositæ, as was indicated in Chapter IX, we must explain the distribution with the land surface of the world as it is to-day.

Concentration at High Levels. The extreme abundance of the Compositæ at high levels is noted in almost all alpine investigations ; it is mentioned by Cassini (I, 18, Tome I, p. 324.), Spruce (69, p. 288), Whymper (73, pp. 199 and 352) and Guppy (IX, 21, Vol. II, p. 238) who quotes Hemsley (37), Hooker and Ball (40) and Schimper (IX, 32) as authorities. Hemsley (37) quotes figures for concentrations along the mountains from the Caucasus to Japan and suggests the pappus mechanism as the cause. Ball (5a) gives 25-30% as the proportion of Composites in the higher Andean flora.

The local dominance of Composites over other plants is well known from common experience with daisies, dandelions and thistles. Interesting cases of complete dominance are given by Darwin (21, p. 113), who mentions beds of the cardoon thistle (*Cynara cardunculus*) "many (probably several hundred) square miles" in extent where "nothing else can now live", and also by Geddes (30), who found the Great Ragweed (*Ambrosia trifida*) covering a ravine with a dense growth of plants 12 to 18ft. high.

Action of Environment. The direct effect of environment on the individual is rapidly becoming one of the most fertile fields in the domain of experimental evolution. Although the origin of new

Linnean species has not yet been effected, changes in the individual in response to definite factors of the environment have been obtained which certainly give greater differences than those between a very large number of taxonomic species.

Some instances have already been mentioned of the effect of injury, food supply etc., on the floral characters: see Molliard (IV, 55-56a) and his explanation of the dioecism of *Pulicaria* (II, 26), also Daniel (IV, 23-24) and the reduction of doubling, Chapter IV, C, under Causal Morphology,

The value of this type of work is recognised by Massart (53), who considers that the effects of the environment are hereditary in some cases at least and, as a consequence, recognises the possibility of a polyphyletic origin for genera or even species. Warming (71, Chap. 100) and the Reports of the Carnegie Institution of Washington furnish abundant references to such experimental evolution. The last chapter of Warming's *Oecology of Plants* is of great interest in this connection (see below Chapter XI). An important point is developed by Harshberger (35) under the term "generic coefficient," which expresses the percentage relation between the number of genera and that of species in any region: *i.e.*
$$\frac{\text{number of genera}}{\text{number of species}} \times 100 = \text{generic coefficient.}$$
 Simple topography, as on the plains, gives a high generic coefficient, while the highly diversified topography of regions such as the Rockies and Andes gives a low generic coefficient.

The subject cannot be dealt with in detail here, but it may be useful to bring together some references. Taylor (70) mentions habitat endemics. Cockayne (17) uses the term *epharmonic variation* in the sense of "a change in its form or physiological behaviour *beneficial* to an organism evoked by the operation of some environmental stimulus. Such a change may be called epharmonic adaptation, as distinguished from such adaptations as cannot be traced to any direct action of the environment" Poweraker (26), who gives some experiments on anthocyan changes in *Ranolia* in response to environment, suggests natural selection as the cause of the origin of cushion-plants but he agrees, in conversation with the writer, that the most probable explanation of his chief problem, "What causes this espalier shape?", lies in the direct action of the heat radiation from the sun-baked shingle on the permeability of the protoplasm of the cells of the under surface of the lateral branches (cp. 68a). This seems to be a clear case of epharmonic

variation. The observations by Foweraker (loc. cit.), Hauri (36), and Schröter and Hauri (60) furnish other examples of similar epharmonic variation in cushion-plants of widely different taxonomic affinities (cp. Schimper IX, 32, pp. 704-716).

It is a significant fact that the first detailed studies of the peculiar insular floras both of New Zealand (15-17) and of the Sandwich Islands (51) have resulted in the emphasis of epharmonic variation. Bews (6-7) dealing with the many peculiar Composites of Natal seems to take the same view although he uses epharmony in Vesque's sense, not in Cockayne's (see below Chapter XI). He writes (7) of the study of epharmony as giving a deeper insight into the causal relationship of environment to plant form.

One of the most extraordinary cases is the change observed in *Cnicus arvensis* by Compton (18) who records that after a flood in the fens all herbaceous plants were killed except *Cochlearia armoracia*, the rootstocks of which sprouted after drainage, and a few specimens of *Cnicus arvensis*, which seemed normal but were attached to the soil by two to three feet of slender, leafless stem, exactly like the woodless stem of a true aquatic. Considering that the thistles probably owe their origin to the heat and dryness of the centre of origin (see below) this epharmonic adaptation in a few weeks to an aquatic habitat is very striking (cp. Warming on *Polygonum amphibium*, 71, p. 371).

Other cases are (a) woodiness in the stem of a marsh plant as the effect of water at 30-40° C (27), (b) various modifications similar to those of arctic plants as the effect of continuous or discontinuous electric illumination (8), (c) desiccation and excessive insolation as the cause of spines (48), (d) the alpine habit in *Senecio Jacobaea* etc. induced by the alternation of low temperatures and darkness with high temperatures and strong insolation (9).

There are also other experimental or observational papers by Oger (56), Harris (33), Dauphiné (22), Constantin (19), Shreve (63-64), Bailey and Sinnott (5) and Jeffrey (43, Chap. XXX).

Age and Area. The Age and Area Law which has been demonstrated by Willis (75-82) is the most important contribution to geographical botany since the *Origin of Species*. As the original accounts and various reviews (20, 23-24, 49, 65, 67) are easily accessible it will be sufficient to note that the formal expression of the law is that "the geographical distribution of a species (*i.e.* the area which it includes within its outer localities) within a fairly uniform country not broken by serious barriers depends, so long as conditions remain constant, upon the age of that species within the country."

The truth and value of this contribution to the subject is obvious when it is noted that the composition of and many other points concerning the flora of a country can be predicted with a reasonable degree of accuracy. It has been applied very successfully to the evolution of the Podostemaceæ by Willis (IV, 93) and has been confirmed for the Gramineæ of Australia by Breakwell (10). Taylor (70) dealing with only 22 endemic species, finds it true in as detailed a fashion as can be expected when dealing with single species, but he transgresses the Willisian dictum that comparisons must be made in groups of 20 or more species. Under these circumstances the exceptions he finds are quite in accordance with expectations. Taylor effects a compromise between the views of Sinnott (65) and Willis. He finds that of 22 endemic species 16 are young and 5 relicts, the remaining case being doubtful. Of the 16 young species 14 are considered to be due to generic or specific instability and 2 to the direct action of the environment (cp. Chap. XI, B).

The theory of "the differentiation of primitive, world-ranging, generalised types in response to the differentiation of their conditions" (Guppy, IX, 22, p. 313) is quite in accordance with the facts of Age and Area, and the idea of the differentiation, especially of insular endemic species, *in situ* is in close agreement with what is known of epharmonic variations. This also solves one of the problems of Age and Area, *i.e.* the occurrence on islands of endemic species of wide spread genera, which are there the only representatives of these genera. If the individuals were confined on arrival to a particular area they would naturally all show the same epharmonic variation, with the result that the original species as represented on the island would be entirely transformed into the new species.

Guppy, however, seems to use primitive in a peculiar sense (op. cit., p. 315) since he classes the Compositæ as primitive! He also appeals very much to geological changes, but no authentic fossil Composites are known below the Oligocene, and the differentiation of climate since has not been sufficient to account for all the differentiation in the family.

Other accounts of phenomena bearing on Age and Area and Differentiation are given by Kroeber (46), Andrews (4), A. Jordan (44, pp. 18-19), D. S. Jordan (45), Lloyd (47) and Samuelsson (59). The most important contribution for present purposes is that by Bentham, who was never an enthusiastic Natural Selectionist. He says (I, 7, p. 481) "The result of the best-founded opinions on this

subject which to my knowledge have been propounded is that a race of plants, be it tribe or genus or species, in its period of full vigour, is widely dispersed, accommodates itself to a great variety of climatological, physical or other external influences, is numerous and varied in subordinate races, as well as individuals, these subordinate races, especially those immediately subordinate, not being separated by wide structural gaps, and not having acquired any marked local characters, but for the most part passing, as it were, into each other, their respective distinctive characters not having yet acquired any marked degree of correlation. On the other hand, a race in a state of decay is represented by subordinate races very distinct in structural characters, of restricted areas, and requiring for their preservation special climatological or other physical conditions, and consequently comparatively few in number Old decaying and apparently expiring races may, however, in some of their branches, owing perhaps a slight change in constitution, habit or external circumstances, start into new life These young progressive races will be very prolific, ready colonisers; and their subordinate races will be generally numerous and so blended together as to defy all positive determinations of their limits, and be variously estimated as subgenera, sections, species, subspecies or varieties." Again writing of the sections of *Vernonia* (I, 7, p. 393) he says "the section *Lepidaplon*, which, rather from its wide geographical range and connections than from its happening to include the species first taken as the type, may be conjectured to be nearest to the original form."

These views, it will be seen, form what is probably the best pre-Willisian account of the relation of Area to Age. But, whereas these are suppositions fairly obvious but unproved, the hypothesis is raised to the status of a fundamental law by the statistical proof furnished by Willis for age within a given country, and its proved extension to absolute age and total area seems to be only a question of time and application.

B. GEOGRAPHICAL DISTRIBUTION OF *Senecio*.

The *Senecioneæ* are indicated in previous chapters as the primitive tribe; the distribution of the chief genus, *Senecio*, is therefore of fundamental importance. If the numerous species of *Senecio* were confined to one locality or even to one continent, it would be difficult to uphold the view that they had been the source, for example, of the *Arctotideæ* in South Africa, the *Vernoniæ* in

South America, and the Cichoriæ in the Mediterranean region. The present investigation, however, shows that the distribution of this genus is quite in accordance with previous suggestions.

Method.

In dealing with the Compositæ the world may be divided into a few large regions, which do not always correspond to the regions delimited in the study of other families.

America is divided thus:—

U. S. A. region:—including Canada and Alaska.

Mexican region:—including Central America and California.

West Indian region:—including all the West Indian Islands in the widest sense,

Andine region:—including west tropical South America.

Brazilian region:—including east tropical South America.

Chilian region:—including extra-tropical South America.

The rest of the world is divided thus:—

Eur-Asiatic region:—including north and central Europe, Siberia and the eastern parts of subtropical Asia.

Mediterranean region:—including south Europe, north Africa and the western parts of subtropical Asia.

Tropical Asiatic region:—including India south of the Himalayas, the East Indies and the Malay Archipelago.

Tropical African region.

South African region:—including extra-tropical South Africa.

Australian region:—including the Australasian islands.¹

These regions serve for a preliminary analysis of distribution and will be frequently referred to later, but in the case of *Senecio* a detailed investigation was made. An alphabetical list of the 2300 species of *Senecio* in the *Index Kewensis* and its Supplements to 1910 was made, including amongst other data the habitat as there recorded. A number of floras and papers (84-135) and the Herbaria at Kew and Edinburgh were then examined for further details. During this investigation about 50 new species were added to the list, so that it is more or less complete. The results of this study are naturally too bulky to be included in the present condensed

¹ A somewhat similar division for mammals is made by Sclater (62) and it is interesting to note that his Cape sub-region connects directly in East Africa with the Saharan sub-region; and that his Western or Arid sub-region includes most of Mexico and the western U.S.A. (see below on Paths of Migration).

account of the family, so that only a general outline of the more striking features will be given.

A map (Plate I, Fig. 29) is given in which the areas of the more important species are delimited by a thick red line, those of less important species with more than a local habitat by a thin red line and those of species which are limited to one state or country by red dots. Accuracy in detail has not been aimed at on account of the small size of the map and because it is unnecessary for the elucidation of the chief points, namely the centre of origin, the paths of migration and the centres of concentration.

The Centre of Origin.

In a number of other widespread genera the centre of origin is clearly indicated by the coincidence of the point of overlapping of the areas of widespread species with the centre of concentration (see Pl. II, 31, Pl. III, 34, Pl. V, 37, 38), but in *Senecio* there is no such indication. Evidence will be given in Chapter XI for the origin of *Senecio* in or about the Bolivian region. The north of South America is the probable centre of origin for most large Angiospermous families (cp. 4). One point which confirms this hypothesis for *Senecio* is the very large concentration of species along the Andes and on the campos, savannahs and the margins of the Brazilian forests, but as there are other equally intense concentrations in South Africa and Mexico this does not form conclusive evidence.

Taking this point as granted in the meantime we can consider the South American species. The species with only a local distribution number in Chili 318, in Peru 66, in Bolivia 56, in Ecuador 36, in Colombia 45, in Brazil 56, in Argentina 36, and in Patagonia 46. These numbers are, however, of little importance for comparison among themselves as they depend perhaps more on our present knowledge of each country than on the actual number of species present. The large number in Chili, for instance, is due to the activity of two botanists Remy (130-131) and Philippi (126-127). It is clear, however, that the Andean is a particularly favourable region for specific differentiation in the genus. On the other hand, not a single species of *Senecio* is recorded from Honduras, our knowledge of the flora of that Central American state having been limited until recent years to a list of some seventy species mentioned by Morris (54). More recent collections have added somewhat to our knowledge of this flora (cp. 41 & 83).

The Paths of Migration.

If the centre of origin is taken as the Bolivian region (see Pl. I, Fig. 29) the study of the widespread species indicates clearly that the path of migration has been southward along the Andes to Fuegia and northwards along the same range towards Central America and the Cordilleran system from Panama to Alaska. Throughout the rest of the world the path of migration is commonly along the mountain ranges, usually above 3,000 ft., frequently above 6,000 ft.

South America. Extending in the southern direction into Chili we get *S. Bridgesii*, Hook. A connection is traced between Chili and the Argentine and between Chili and Patagonia. There are two species, *S. Smithii*, D.C. and *S. candidans*, D.C. which are of interest. The former extends from southern Chili into the Magellan and Fuegian regions and to the Falkland Islands. The latter occurs in Fuegia and the Falklands. The Falkland Islands are about 300 miles from the nearest land, but, instead of raising a very hypothetical land-bridge to explain the distribution, we can point with some certainty to the westerly trade winds and remind the reader of the fact demonstrated in the previous chapter that the minimum wind for dispersal to any distance of an average fruit of *Senecio vulgaris* is 1.5 m.p.h. In the region in question we have a wind of the necessary velocity in the proper direction and sometimes though not always the air has the necessary low relative humidity.

Extending northwards we have *S. medullosus*, S.B. from Bolivia to Colombia, *S. superbus*, S.B. from Peru to Colombia, and *S. rhizocephalus*, Turcz. from Ecuador to Colombia, while other species with smaller ranges connect other parts of the Andine path.

South America to North America. The connection between the two halves of the American continent is made by two species, *S. decompositus*, Hieron. and *S. formosus*, H.B.K. The latter occurs in Bolivia, Colombia and Mexico, the former in Venezuela, Colombia and Mexico. Greenman (100) also mentions *S. ledifolius*, D.C. as connecting North and South America.

Central America to North America—The bridging species between these two regions are *S. lanicaulis*, Greenm. and *S. Aschenbornianus*, Schau., the latter occurring at levels over 6000 ft. on the Central American mountains.

North America. The widespread species in this region usually belong to the Cordilleran flora, and there is a considerable affinity between Texas, Arizona, California and Mexico, so much so that

these states are included in the "Mexican" region by Bentham, (I, 7). The most important species are *S. lugens*, Rich., *S. canus*, Hook. and *S. triangularis*, Hook., which occur all along the Cordilleran system from California to the Arctic region, each species showing a number of forms and occurring sometimes as high as 12,000 ft. or, especially in the Arctic region, coming down to sea level. These three species also extend eastward to a varying degree, as far as Saskatchewan, Manitoba and Iowa. *S. Fremontii*, T. & G. does not extend north of British Columbia, but occurs further south in Mexico, while *S. eremophilus*, Rich., which extends to the Mackenzie River, is confined in its southern area to the eastern spur of the Cordilleras.

The northern region is covered by *S. Hookeri*, T. & G., which extends from the Arctic regions southwards only to the high northern Rockies. The eastern path along the Appalachian system is indicated by *S. lobatus*, Pers., which extends from Mexico to Florida, Carolina and Illinois, and even more clearly by *S. suaveolens*, Ell., which occurs along the mountains from Maine to Florida.

The gap between the Appalachian species in the east and those of the Cordilleras in the west is bridged by *S. aureus*, L., which with many variations in form extends from the west coast to the east coast and from Newfoundland, the North-west Territories and Alaska in the north to Mexico and Florida in the south. Other species with smaller areas link up the parts of both eastern and western paths.

North America to Asia and Europe—The Behring Strait presents no impassable barrier to fruits which can be blown long distances by winds of less than 4 m.p.h. and the result is a strong connection between arctic America and Siberia. *S. Pseudo-Arnica*, Less., extending in America from Maine and Newfoundland to Alaska, occurs also in northern Asia. Three other species make use of this "Alaska-Siberian bridge": the most wide spread of these is *S. palustris*, Hook., which occurs all over the northern temperate and Arctic regions including Greenland. The other two are *S. resedifolius*, Less., and *S. frigidus*, Less.: the last like *S. Pseudo-Arnica* occurs near the coast and in habit it is similar to that species. The Alaska-Siberian bridge is mentioned by many writers (see 55, 118, etc.).

Asia. The first path to be noted in Asia lies along the Altai and Thian Shan Mountains from Siberia to Turkestan (cp. 25). This

is shown by *S. Ledebouri*, S.B., and *S. altaicus*, S.B., and is extended along the mountains of Afghanistan and Persia to the Persian Gulf by *S. dubius*, Ledeb. The second path lies along the east of Mongolia and Tibet by way of the Yablonoï, Khin-gan and Sin-ling Mountains from Siberia to the eastern Himalayas. This path is taken by *S. Ligularia*, Hook. The eastern Himalayan region is connected with the southern Chinese provinces by at least seven species of *Senecio*, and *S. scandens* extends beyond that region to Ceylon, the Neilgherries and Burma. A further extension from the eastern Himalayas is shown by *S. araneosus*, D.C., which occurs from China through Sikkim to Ceylon and Java. India and Java are also connected by *S. tenuifolius*, Burm. Other species with smaller areas again link up the parts of both the eastern and western paths through Asia.

Asia to Europe. The extension of the west Thibetan path into Europe is shown in detail by *S. sibiricus*, L., which occurs from Dahuria and the Yablonoï via the Altai Mts. and Turkestan, the extension being along the Caucasus and Carpathians to the Alps. Part of this path together with a much wider extension of area into the plains of the Eur-Asiatic region is covered by *S. sarracenicus*, L., *S. paludosus*, L., *S. sylvaticus*, L., *S. erucifolius*, L., *S. præaltus*, Bertol., and *S. brachyæthus*, D.C. The Siberia-Caucasus-Carpathians part of the path is covered by *S. capitatus*, Steud., and other shorter parts by other species.

Asia and Europe to Africa. The further extension of the west Thibetan path into Africa is shown in detail by *S. coronopifolius*, Desf. This species occurs all over Europe and northern Asia, and through Turkestan, Afghanistan, Baluchistan, Persia, Syria, Palestine to Egypt, the Sudan and Abyssinia. *S. erraticus*, Bertol., and *S. Jacobæa*, L., extend this area to north-west Africa, including Algeria and the region north of the Atlas Mts.; the former species extends even to the Azores.

An interesting species is *S. Decaisnei*, D.C., which, although it extends north-east into Asia only as far as Afghanistan, occurs also in India, and from northern Arabia across Africa to Morocco and the Canary Islands, and south through Nubia, probably as far as South Africa. This connection between north and south Africa is confirmed by *S. maritimus*, L., which occurs commonly in the Mediterranean region and in South Africa. In addition to the above-mentioned species *S. Schimperii*, S.B., links up Arabia and Abyssinia, while *S. arabicus*, L., connects Arabia, Egypt and

Nubla. There are also a number of species, such as *S. nebrodensis*, L., *S. vernalis*, Wald., and *S. squalidus*, L., which are widespread within the Mediterranean region, thus linking up Asia, Europe and Africa.

Europe to Africa. A connection is made between Europe and Africa at the western end of the Mediterranean by a number of species with areas varying from that of *S. crassifolius*, Willd., which extends from France and Spain to Italy, Sardinia, Algeria, Morocco and the Canary Islands, to that of *S. Auricula*, Bong., which occurs only in Spain and Algeria.

Africa. The path of migration in Africa is clearly along the mountains of the east coast. The first step is shown by *S. Senecioides*, S.B., which extends from Abyssinia into Galla. The path is extended to Mozambique by *S. subscandens*, Hochst., and to Natal and the Transvaal by *S. picridifolius*, D.C. The southern part is covered by *S. paucifolius*, D.C., which extends from the Zambesi into the east and south of Cape Colony, and the northern part is covered by *S. longiflorus*, S.B., which extends from Abyssinia to the Kalahari Desert. Other species again form smaller links in the chain.

Two interesting species in the west are *S. Mannii*, Hook., and *S. clarencianus*, Hook, which both occur in the Cameroons and Fernando Po. This is a case similar to that of Fuegia and the Falkland Islands species, but the distance between the two localities is only about 70 miles. A more striking case is *S. Leucadendron*, Benth., which occurs on St. Helena and on Prince's Island,¹ the distance in this case being nearly 1,500 miles. In this region the south-east trade winds may well be the distributing agent of the pappose fruits, and in view of the evidence given in Chapter IX, a journey of 1,500 miles over the sea is not improbable for a fruit of the *Senecio* type.

Centres of Concentration.

As the basal genus of the family it is to be expected that *Senecio* will have a considerable share in the predominance of the Compositæ in the higher regions of the mountains throughout the world. There are many species with very limited areas, but as shown above there are also the usual proportion of widespread species. It will be obvious from the distribution of the red dots on the map (Fig. 29) that these local species are most abundant along

¹ This extension to Prince's Island is supported only by one specimen in Herb. R.B.G., Edinburgh, concerning the collection of which there is no detail known.

the ridge which extends around the Pacific and Indian Oceans from Fuegia to South Africa.

In South America 70% of the species of *Senecio* occur in the Andes; the percentage is somewhat lower in North America, but some idea can be gained of the development of *Senecio* in the Cordilleran system from the descriptions by Harshberger (34). *Senecio* and *Gutierrezia* (op. cit., p. 224) are the dominant genera of the mesas in the autumn. *Senecio* again forms a considerable part of the rich vegetation of the hanging meadows on the hill-sides (op. cit., p. 260) and is mentioned among the important genera of most Cordilleran regions. Weberbauer (72, p. 111 and p. 113) also gives *Senecio* first place among the genera with many Andine species. Greenman (100), who gives a general account of the 22 sections of North and Central American species of *Senecio*, also notes that the greatest development of the genus in both North and South America occurs on the mountains. The abundance of Composites in these and similar regions frequently impresses non-botanical writers, e.g., Petrocokino (57) mentions "fields golden with a kind of yellow marguerite" in the Andes of Bolivia.

A noteworthy point is that Honduras is a complete blank and Harshberger (op. cit., p. 663) mentions no *Senecio* in the Guatemalan region, which includes Honduras, nor is there any endemic species recorded from Nicaragua or San Salvador (cp. Hemsley, 107).

In the arctic and subarctic regions there is naturally no abundance of local species. The next region of concentration is in China, especially the south-eastern region, which is closely connected with the eastern part of the Himalayan concentration. The western part of the Himalayan concentration connects with a smaller development of local species along the Hindu Kush and Elburz Mts. This in its turn leads on to a stronger development along the Caucasus and through Asia Minor to the Balkans, Carpathians, Alps and Pyrenees.

Still following the path of migration along the mountains there is some slight development of local species in Arabia, connecting with a larger development in Abyssinia. The region of concentration extends in some degree along the mountains of east tropical Africa, culminating in the 54 endemic species of *Senecio* in Madagascar and the 280 local species which have been recorded for South Africa.

Rather isolated developments of local species occur in Australia and New Zealand, which are connected by *S. laetus*, Forst., and *S. odoratus*, Horn.

The six Javan species and the five Phillippine species indicate the two probable paths for the Australian supply of *Senecio*, the one from India *via* Burma and the Malay Peninsula and the other from China, *via* the Phillippines and East Indies (cp. Gibbs, 31, on New Guinea as the source of Australian types).

Ecology.

It will be clear from the above considerations that the regions of concentration for local species lie along the paths of migration as shown by widespread species, and that both are more or less co-extensive with the 3,000 ft. level throughout the world. The reason is to be sought in the aut-ecology of the genus, but as this forms the subject of a more extensive account now being prepared it will be sufficient to indicate briefly some of the more salient points,

The genus *Senecio* includes herbaceous annuals, biennials and perennials, which may be anything from aquatic to xerophytic in structure, also semi-shrubby and shrubby forms, which are erect or climbing, and trees of various growth forms.

The weedy type is the commonest and occurs in all the mesophytic habitats, but there are a number of distinct types which are characteristic of the regions where they occur. In common with many other Compositæ these weedy species of *Senecio* show a general tendency to develop a single, rather large capitulum, instead of the common branched inflorescence, as the altitude of the habitat increases. This type, sometimes called the *Arnica* type, occurs along the very high regions of the Andes and Cordilleras, and also lower down in the Arctic region. *S. Pseudo-Arnica* and *S. frigidus* have this uni-capitulate habit, while *S. resedifolius* is similar but smaller and more like *Bellis perennis*. Along the west Thibetan path this *Arnica* type is replaced by species which with the same general structure are of ranker growth with medium-sized capitula arranged in corymbs. Along the east Thibetan path the *Arnica* type is replaced by larger species with racemes of large capitula. Further south these two types are replaced by less rank but similar growth forms.

The shrubby species of South America are scandent in Brazil but usually erect in the Andes, and show several peculiar types.

Bolivia has a number of very dwarfed shrubs, only an inch or two high, the majority, however, are erect and from six inches to two feet high, as in the other Andine regions. An interesting spiny species *S. spinosus*, D.C., occurs in the Lake Titicaca region, where the dryness and excessive insolation (cp. Sect. A above) may be judged from the fact that the lake is gradually drying up by evaporation although supplied by seven rivers which are of considerable volume during the rainy season (52).

The shrubby forms of India and China are scandent in open forest or at the edges of denser forests as in Brazil; the erect shrubs are more or less confined to the Deccan and the mountains above the tree level, as in South America.

In Africa shrubby erect and scandent forms occur along the mountains from Abyssinia to Cape Colony, and a number of trees occur at high altitudes; of these none is more striking than *S. adnivalis*, which forms an open forest on Mt. Ruwenzori (14) similar to that formed by *Espeletia grandiflora* on the Paramos of Colombia (cp. I, 42, Fig. 109 and Goebel 32, Teil II, Pl. X and p. 17). In South Africa the peculiar shrubby form is more coniferous or "abietoid," and is to be compared with ericoid species of the same latitudes in the Andes.

The shrubby species of New Zealand are also of a distinct and peculiar type, but most of the Australian arborescent species are more allied to the South African forms. Each region in fact has its characteristic type of shrubby *Senecio*.

From the account given in Chapter IX it will be clear that the fruit dispersal of *Senecio* is easy on grassy plains and on mountain sides, both above the tree level and in the unwooded regions which are common below a certain altitude (cp. 34, p. 243 and I, 7, p. 484). The tundra zone of the northern latitudes also holds no obstacle to the dispersal of pappose fruits and the wide areas of the Arctic species is the result.

In migrating from its place of origin along the mountain ranges of the world *Senecio* has obviously followed the line of least resistance and avoided all forests and low-lying regions where fruit-dispersal by wind becomes distinctly problematical. The diversity of conditions along such a path (cp. 35) as well as constitutional instability is probably responsible to a great extent for the concentrations of local species which occur at all favourable points.

Conclusions.

Taking Bolivia as the still hypothetical centre of origin for

Senecio it is clear from the detailed study of the genus, of which the above is a very meagre and fragmentary account, that its history can be epitomised somewhat as follows. The genus, arising in the Andes, spread comparatively rapidly (cp. Willis, 82, p. 342.) along the unwooded regions of the mountain ranges of the world ; while the floral structure which characterises the genus remained practically the same, the extreme diversity of conditions combined with a marked constitutional instability in the vegetative structure produced in each region several distinct variations in habit and a large number of local species. Because of this free reaction of the vegetative part of the *Senecio* plant to its environment there is no species which completely covers the range of the genus. *S. vulgaris* is cosmopolitan but has been largely introduced from Europe. Instead of a species we have the weedy *type*, which is cosmopolitan, and also various species with wide areas of distribution, a few of which taken together cover the chief regions occupied by the genus.

Finally it is abundantly clear that the geographical distribution of *Senecio* is quite in accordance with the view that a number of tribes have arisen from this genus in widely separated regions of the world.

C. GEOGRAPHICAL DISTRIBUTION OF THE TRIBES.

Although not up-to-date, Bentham's statistical summary (I, 7) of the geographical distribution of all the genera of the Compositæ remains sufficiently accurate for a general view of the distribution of the tribes and sub-tribes. The centres of origin and paths of migration, however, cannot be deduced from his table with any certainty. An analysis was therefore made of the distribution of some fifty widespread genera, including 8,600 species, by similar but not such detailed methods as were used for *Senecio*. Maps were made and the centres of origin and paths of migration were traced. In these maps a line around a country with a number included is used where the distribution within the country is not given in detail, and many dots are used where the map is too small for the useful employment of lines which indicate wider areas. Genera from all the tribes except the Calenduleæ and Arctotideæ were examined. Bentham's table was used in some cases to elucidate the centres of concentration of the sub-tribes and the results will now be discussed.

Senecioneæ. As the basal tribe the Senecioneæ have been studied specially and the distribution of all the genera in each

sub-tribe is given (Fig. 30). The close similarity between this map and the previous one (Fig. 29) will be obvious at a glance. The local genera occur in the more important regions of concentration for *Senecio*. The widespread genera follow the mountain ranges of the world and the more or less treeless arctic zone, just as the widespread species of *Senecio* do. The exceptions are (a) *Gynura*, which connects tropical Asia with Australasia, thus supplying a link which is missing in *Senecio*, (b) *Erechtites*, which connects America with Australia, and (c) *Werneria*, which shows a curious discontinuous distribution from the Andes to the Himalayas and Abyssinia.

The centre of origin for the Liabinæ is Colombia or Mexico. Hoffmann's African genera (I, 42) require reconsideration. The Tussilagininæ are seen to be the further development of the *Arnica* and *Ligularia* types of the northern regions, originating probably in Siberia and spreading all over the arctic and sub-arctic zone. The Senecioninæ, the basal sub-tribe, is characterised by a number of widespread genera, the local genera occurring in the regions of concentration shown by *Senecio*. The Othonninæ are clearly of South African origin extending north along the mountain ranges to Abyssinia; the genus *Werneria* requires special consideration.

Cichorieæ. All the sub-tribes here, with the exception of the insular Dendroseridinæ, have their centres of concentration and region of overlapping of the areas of widespread species in the Mediterranean region. The centre of origin is thus clearly defined, but the paths of migration are not so clearly marked as in the Senecionæ. *Lactuca* may be taken as the type of distribution shown by the widespread genera (Fig. 31).

Details of the distribution are not necessary to show that from the Mediterranean the genus has spread to America and Africa by the same route as that by which *Senecio* arrived. *Hieracium*, *Hypochaeris* and other genera have spread further along the mountain ranges of the world, extending into the Chilean Andes; while *Sonchus* has spread still further, extending to Australasia.

Calenduleæ. Most of the genera of this tribe are confined to South Africa, but *Calendula* and *Dipterocome* are Mediterranean, while *Eriachænum* is Chilean. The systematic position of the last genus requires reconsideration. *Tripteris* extends into Tropical Africa. There is very little doubt of the South African origin of the tribe.

Arctotideæ. Except for the small genera *Gundelia* in the Mediterranean region and *Cymbonotus* in Australia, the Arctotideæ are South African with a very slight extension into tropical Africa. It is interesting to note that this northern extension occurs chiefly in *Ursinia*, and to a lesser degree in *Arctotis* and *Berkheya*.

Anthemideæ. The distribution of this tribe is peculiar. There is a distinct centre of concentration for both sub-tribes in the Mediterranean region, but the Chrysanthemidinæ shows a subsidiary concentration in South Africa, with more genera but fewer species than in the Mediterranean concentration. This is a case where the diversity of conditions gives a high generic co-efficient apart from the differentiation at the centre of origin.

The map (Pl. II, Fig. 32) illustrates the point; there are quite a number of small genera endemic in South Africa, but the areas of most of the widespread genera of both sub-tribes overlap in the Mediterranean region. The primary importance of this geographical centre is clearly shown when maps are made of the species in the larger genera. These practically all show a marked Mediterranean centre for local species and for overlapping of the areas of the widespread species, notably so in *Achillea*, *Chrysanthemum* and *Artemisia*. The paths of migration are the same in these and most other genera of the Anthemideæ as in *Senecio*.

Inuleæ. A number of genera in this tribe have been examined by the map method, but on account of the limitations of space, only *Gnaphalium* is given in the map (Fig. 33), while the centres of concentration for the sub-tribes are indicated. It has been suggested (Fig. 7) that the Gnaphaliinæ are the primitive sub-tribe, and the Helichryseæ the primitive section. When examined geographically there is little doubt that *Gnaphalium* is the primitive genus, so that the relative positions of the two sections of the Gnaphaliinæ should be reversed. This will be discussed later.

A map of all the genera of the Inuleæ shows that a marked proportion of the widespread genera belong to the Euguaphalieæ. The map of the species of *Gnaphalium* shows centres of concentration and paths of migration corresponding closely to those of *Senecio*. It is of interest also that several species of *Gnaphalium* are more widely distributed than any one species of *Senecio*. This is probably due to a more stable constitution, corresponding to the more advanced evolutionary position of the genus. These matters

are discussed below (Sect. D). The Helichryseæ are clearly South African in origin, as are several sub-tribes (see Fig. 33).

The only other wide spread sub-tribes are, (a) the Plucheinæ, which, with their chief centre in tropical Africa, have subsidiary centres in tropical Asia and Australia, and also extend into all the American regions, (b) the Filagininae, which, although rather diffuse and extending to Mexico, have a distinct centre in the Mediterranean region.

The Inulinae, although fairly widespread in the Old World, are markedly Mediterranean in origin, as is shown by maps of the species of the widespread genera, especially *Inula* and *Pulicaria*. Another point of interest is the centre of the Bupthalmineæ at the eastern end of the Mediterranean region.

Cynareæ. The centre of origin, as indicated by the coincidence of the region of concentration of local species with the region of the overlapping of the areas of the widespread species, is nowhere more clearly indicated than in *Centaurea* (Fig. 34). The centre for all the sub-tribes is at the eastern end of the Mediterranean region, and the same type of map is shown by all the wide spread genera of the Cynareæ. The paths of migration are the more arid regions along the mountain ranges, but this is shown better by *Cnicus* and *Echinops* than by *Centaurea*. Only the last genus extends to Chili but *Cnicus* extends to Mexico and *Saussurea* to the U.S.A.

Mutisieæ. There is in this tribe no genus common to the Old World and America with the exception of the South American genus *Trichocline*, which has one species in Australia. An analysis of all the genera in each sub-tribe shows that the chief centre for each is in South America (Fig. 35). The Nassauviinae and the Barnadesiinae are confined to America, but the other three sub-tribes have some genera in Africa. The two geographical groups of genera are illustrated by two of their most wide spread members, *Trixis* and *Gerbera*. *Trixis angustifolia* extends north to California and Arizona, while *Gerbera Anandria* extends to north Siberia. The paths of migration are the same as in *Senecio*, but a gap exists between Siberia and California. The Nassauviinae show a marked concentration of both species and genera in Chili; although the local species of *Trixis* are chiefly Mexican, there are a number of local species in Brazil, and the commonest species, *T. divaricata*, is South American.

Vernonieæ. The type of distribution here is quite a simple one. The centre of concentration is in Brazil, and there is an

inter-tropical connection. This applies equally to *Vernonia* (Fig. 36) with 948 species and the bridging sections *Hololepis* and *Lepidaploa*, and to *Elephantopus* with 24 species and the bridging species *E. scaber*. In both genera there is also an extension north into the U.S.A. region. A path of migration across the islands of the Pacific is indicated by the above-mentioned sections of *Vernonia*, by *E. scaber* and by *V. cinerea* (11).¹ The stretch of ocean between Peru and the Marquesas is not an impassable barrier, given a pappose fruit and the south-east trade winds (cp. Chapter IX). The occurrence of *V. Zeylanica* in Ceylon and Madagascar is probably explicable in the same way by a pappose fruit and the monsoons, although this case requires further examination. An Atlantic path of migration is indicated by *Sparganophorus Vaillantii*, which connects east tropical America with west tropical Africa.

Except for *E. scaber* and one other species in Senegambia the Lychnophorinæ are confined to America, but there are a number of African genera in the Vernoniinæ.

Astereæ. The distribution of the primitive genus, *Solidago*, is typical (Fig. 37). A concentration in the U.S.A. region is clear, and the path of migration is that of *Senecio*. This point, however, is much clearer and more distinct in the maps of *Aster*, *Erigeron* and *Conyza*, which are too complex for inclusion in the present account. The centres of the sub-tribes are indicated by letters. The Homochrominæ extend south into the Mexican region to a marked degree. The Bellidinæ are rather diffuse, occurring in all the regions of the world, as do also the Heterochrominæ with a chief centre in the U.S.A. and other concentrations in Mexico, South Africa, Australia and the Eur-Asiatic regions. The Conyzinæ are markedly African and the Grangeinæ occur chiefly in tropical Africa and Asia. The Baccharidinæ are another diffuse group but are chiefly Andine.

Eupatorieæ. For the present purpose *Mikania* and *Eupatorium* have been united into the basal group which has been referred to previously. The distribution of this group (Fig. 38) shows the characteristics of the Eupatorieæ very well. There is a concentra-

¹ A migration to the Sandwich Islands from the Australian and Malay-an regions as well as from America is proved by Campbell (12), and was previously suggested by Hooker (IV, 39), who gave only general evidence. Hutton's idea of a continental bridge across the Pacific in Tertiary times (42) is modified by Macloskie (118) into an "archipelagian" bridge from New Guinea and New Zealand to Chili, very similar to but perhaps more developed than the existing Pacific archipelago.

tion in the Mexican region, but the Andine and Brazilian regions show others almost equally well developed. There is a tropical connection by *Mikania scandens* and also by *Ageratum conyzoides*. In addition there is some indication both in its present and its Pliocene distribution of the use of the Alaska-Siberian bridge by *Eupatorium*.

The Piqueriinæ are best developed in Mexico and the Andes, the Adenostylinæ in Mexico and the U.S.A. regions. The main sub-tribe, Ageratinæ, have the distribution of the *Eupatorium-Mikania* plexus, extending more or less into all the regions of the world.

Heliantheæ. The Verbesininæ have been suggested as the primitive sub-tribe (Fig. 7), and *Spilanthes*, with type 4 stamens, type IV style, setiferous aristæ in the pappus and a sub-biseriate involucre seems a probable primitive genus. The distribution of this genus is, therefore, given (Fig. 39) together with the centres of the sub-tribes.

The detailed distribution of this tribe is somewhat complex, as there are several more or less cosmopolitan genera, but the *Spilanthes* type of distribution is common among these widespread genera; *Ambrosia*, *Xanthium*, *Siegesbeckia* and *Eclipta* are examples, the last two belonging to the same sub-tribe as *Spilanthes*. A northern connection *via* the Alaska-Siberian bridge in addition to the usual tropical one is indicated in *Bidens*.

All the sub-tribes, except the peculiar Petrobiinæ, have a Mexican concentration. The Verbesininæ and Coreopsidinæ extend into all the regions of the world. The Lagasceinæ, Madiinæ and Zinniinæ have only a slight extension from Mexico, and the other sub-tribes are practically confined to America, extending more or less strongly into the Andine and Brazilian regions.

Heleniææ. All the sub-tribes of the Heleniææ are practically confined to America, and *Porophyllum* (Fig. 40) is taken as one of the widespread genera, although it is probably not the most primitive. *Jaumea*, *Flaveria* and *Cadiscus* are the only genera which extend to the Old World, but there is only one species of each outside America. The distribution of the Tagetinæ is very closely similar to that of the Galinsoginæ, both sub-tribes developing in the same regions and almost to the same degree. There is a distinct extension to the Chilian region in the Baeriinæ and the Heleniinæ, but only one or two species of the Jaumeinæ and Flaveriinæ extend to that region.

Ecology of the Tribes.

The causal relationship of a number of ecological conditions to the arborescent habit, the spiny habit, the cushion and espalier habit, and other plant forms in the Compositæ, can be taken as proved to a degree of comparative certainty.

Scapigerous Perennials. In the grasslands herbaceous perennials are the chief type and, as in *Senecio*, this type tends to become dwarfed, scapigerous, and finally uni-capitulate in the alpine and arctic regions. The origin of the *Cremanthodium* from the *Ligularia* type of *Senecio* (see Chapter II, E) seems to be almost entirely due to the arid alpine conditions of the screes which form the typical habitat of that genus.

Scramblers. The climbing or scrambling habit is clearly due to the direct action of the environment (see Henslow, 38, p. 44) and Cockayne gives some very good evidence for this explanation (15, p. 21). The presence of open forest or scrub is necessary for the development of the typical Composite scramblers. These are most abundant on the western margins of the Brazilian forests and in the tropical African scrub.

Erect Shrubs. The erect shrubby forms of the Andes are probably the effect of an aridity of environment which does not obtain in the Cordilleras, with the result that the shrubby Composites are not so common in the northern region. Quite a number of genera with many arborescent species in the Andes are represented in the Cordilleras by perennial herbs. The erect shrubs reappear at high altitudes in tropical Africa and more abundantly in South Africa (cp. 6-7), Australia and New Zealand, where the ecological conditions are somewhat similar to those of the Andes. The shrubs peculiar to so many oceanic islands are probably also the result of the direct action of aridity, wet and cold, or hot and dry conditions (cp. 50-51).

Trees. The large shrubs and trees are obviously the extreme development of the shrubby condition. These trees usually occur as more or less isolated specimens high up on the mountain sides where there are open associations and consequently very little competition, and where all the ecological conditions tend to slow growth and lignification. The trees of the oceanic islands have long been objects of interest, usually regarded as relics of an ancient flora, but in the light of the new views on the origin and dispersal of species they are to be considered as more or less recent species which have become arborescent under the influence of external conditions. In addition most of these species have lost

the means of wide dispersal possessed by their ancestors, and the localised distribution may be due to any or all of the following facts : (a) the species is recent, (b) the fruit is epappose, (c) the plant does not bear fruit until several years old, (d) the supply of fruits from the few specimens which represent the species is not sufficient to cover all the casualties sustained in travelling across the wide stretches of ocean, and in the attempt to establish the species in a region usually quite different ecologically and already well stocked with other plants.

These various forms, scapigerous perennials and arborescent species, occur in almost every tribe and their detailed evolution in each group is very interesting.

Spiny Forms. It is clearly easier for the appropriate ecological conditions to produce spines from leaf structures which are already reduced. The result of this is seen in the spinescent involucre bracts characteristic of the Cynareæ and common in the Bupthalamineæ (Inuleæ), Gorteriineæ and Gundeliineæ (Arctotideæ). Spiny leaves occur also in the above-mentioned groups and in *Scolymus* (Cichorieæ). All these spiny forms occur either in the Karroo (Gorteriineæ) or in the semi-desert area at the eastern end of the Mediterranean region.

Aquatics. Although many Composites, but not a large proportion, are marsh plants there are very few aquatics (15, p. 17 and 1,43), and, as these belong to various tribes, any phyletic value they possess is strictly limited. It will be sufficient to indicate the possibilities of the basal genus as shown by *Senecio hydrophilus*, Nutt, which grows in wet ground or even in brackish water, and the possibilities of the most advanced tribe as shown by the extraordinary production of an aquatic stem by a species which owes its spiny condition to the excessive insolation and dryness of the original habitat of its ancestors (see Sect. A and 18).

D. THE PHYLOGENETIC SIGNIFICANCE OF GEOGRAPHICAL DISTRIBUTION.

Absolute age is not considered at all by Willis in his exposition of the law of Age and Area. He limits his conclusions to age within the given country. Although proved only for age within the country the law receives its logical expansion to absolute age from Sinnott (65, p. 214), who says "there is doubtless much truth in Willis's main contention that, other things being equal, the longer a species lives, the wider the range it will cover." In this way we return to the views expressed by Bentham (Sect. A).

Physiological Differentiation and Restriction of Area. Considering the list given by Willis (78, p. 206) of causes which may modify the application of the law of Age and Area, and considering also Bentham's remarks quoted in Section A, we can trace an underlying principle which may be expressed as above. In a paper read before Section K of the British Association in 1916 (67) the writer applied the law of Age and Area to absolute age and total area and indicated the relation of physiological differentiation to restriction of area somewhat as follows: "We find in the *Compositæ* that the morphologically higher or more differentiated groups are well developed in the same regions as their morphologically lower or less differentiated ancestors. As these groups of ancestors and descendants occupy the same areas and show their maximum concentrations in these areas it is evident that the survival of the fittest in so far as it applies to morphological development has not exercised any very rigorous action, otherwise the ancestral groups would have been eliminated by their more highly developed offspring."

"On the other hand we know nothing very definite about the physiological differentiation of these groups and from analogy it would seem probable that within the limits of any particular family a morphologically primitive plant would be physiologically primitive and that a morphologically advanced plant would be physiologically highly differentiated also. The result of this would be that, although the higher forms would be more successful in those areas peculiarly well suited to their physiological constitution, this advantage would be more or less counterbalanced by the greater range, or greater choice of habitat, which would be enjoyed by the lower forms on account of their lack of special physiological differentiation. This compensation of the advantages of adaptation to one habitat by the power of living in many different habitats seems the most probable explanation of the continued existence in such profusion of *Senecio*, the primitive genus of the family."

"Of course, morphologically reduced forms must be carefully distinguished from the primitive forms, as these reduced forms would probably have a relatively highly differentiated physiological constitution." It should be further noted that a genus with an unstable constitution, (*i.e.*, abnormally susceptible to environmental conditions and liable to spontaneous mutations) will probably not show a species covering the range of the genus, while a more stable genus may have this characteristic (cp. 75, p. 336).

Guppy in the following year independently expressed the same

principle thus :— " That differentiation and decrease of range go together is a principle that seems to prevail through the whole plant world " (IX, 22, p. 314).

Age and Area. The most striking example of the action of the law of Age and Area is the world-wide distribution and numerous centres of concentration of the basal genus *Senecio*. No genus in the family has a distribution at all approaching that of *Senecio*, except *Gnaphalium*, the basal genus of the Inuleæ-Cynareæ branch, which is of comparatively ancient origin. Along this line we can follow the genus *Gnaphalium* in its period of full vigour and the gradually higher physiological differentiation and restriction in area which culminates in the Bupthalthinæ; then from this "apparently expiring race" we have the vigorous "young progressive race" starting into new life in the Cynareæ with all the characteristics given by Bentham (see above Sect. A). The significance of these small groups, such as the Bupthalthinæ and Liabinæ, which give much larger and more widely spread groups will be made clearer in the following chapter, Sect. B.

The wide distribution of some genera of the Heterochrominæ, and Verbesininæ also illustrate the principle of Age and Area. Other examples are *Liabum*, the *Eupatorium-Mikania* plexus, *Vernonia*, *Trixis* and *Ursinia*; in fact the primitive genus in almost every sub-tribe and the primitive sub-tribe in almost every tribe, in addition to the primitive genus of the whole family, show the greatest area occupied by the oldest member of the group. There are exceptions such as the Bupthalthinæ and Nassauviinæ, but these are peculiar groups, and their rejuvenescence to give larger, wider spread, more prolific races is in accordance with the general life history of a race as given by Bentham.

One point, however, requires consideration. Bentham regards these "decaying races" as ancient, but the facts of the individual cases show that they are more probably derivative races, arising comparatively recently from the widespread vigorous races. In Bergson's phraseology they are the last, small reverberations of the explosions which scarcely interrupt, and certainly do not stop, the progressive unrolling of the main theme. As a rule one genus in each restricted sub-tribe is closely allied to the immediate ancestor of the sub-tribe and, retaining the relatively primitive condition, physiological and otherwise, is capable of expansion, while the other more distant derivatives remain restricted more or less to their original sphere. Whether these restricted forms are really

dying out or not is uncertain; the only relevant evidence is that given by Willis for the absence of any considerable dying out in the Angiosperms (77).

If the facts of distribution of the sub-tribes as given in the maps and Section C are compared with the phyletic scheme (Fig. 7) it will be seen that only in a very few details does the scheme fail to answer the test of geographical distribution.

Senecioneæ. The Senecioninæ have all the characteristics of a primitive race, either from the "Age and Area" point of view or from Guppy's "Differentiation" point of view. The Liabinæ (Fig. 30) in the Andine region, the Tussilaginæ in the Asiatic region, and the Othonninæ in South Africa all arise at points where specific differentiation in *Senecio* is well developed.

Cichorieæ. The Mediterranean centre for the majority of this tribe and the comparatively restricted area of most genera and species is in accordance with its suggested recent origin from the Mediterranean Senecioninæ.

Calenduleæ. The South African centre for this tribe and its marked restriction in area, in addition to its close similarity to the Senecioneæ in morphology and physiology, suggest an origin from the South African Senecioninæ at a date even more recent than that of the origin of the Cichorieæ.

Arctotideæ. The South African centre and the distribution of this tribe suggest an origin very similar in source, time, and place to that of the Calenduleæ. The wider areas of *Ursinia*, *Arctotis* and *Berkheya* confirm the positions of the Arctotidinæ and Gorteriinæ, while the restriction in area of *Gundelia* and *Platycarpha* confirms the position of the Gundeliinæ.

Anthemideæ. The Mediterranean centre and wide distribution of a number of genera in this tribe suggests an origin from the Senecioneæ of that region at a time previous to the origin of the Cichorieæ. The wider distribution and larger development in South Africa of the Chrysanthemidinæ (Fig. 32) confirm the suggestion made in Chapter IV, F, of the primitive position of at least the main genera of that sub-tribe.

Inuleæ. The Gnaphaliinæ are confirmed as the primitive sub-tribe, but the Eu-gnaphalieæ are shown to be the primitive section of the sub-tribe. In various morphological characters the Helichryseæ as a whole have appeared to be more primitive, but at this stage it is permissible to compare the main genera rather than the groups as a whole, because the smaller genera are seen to be little

more than local variations of the larger genera. *Gnaphalium*, with a wide distribution (Fig. 33), with type IV style, type 10 stamens, simple setose pappus and foveolate or naked receptacle, is obviously more primitive than *Helichrysum*, which does not extend to America and which has type IV style, type 13 or 14 stamens, simple setose pappus, and a naked, foveolate or alveolate receptacle. Five of the Old World genera of the Eu-gnaphalieæ extend to America and only one Old World genus of the Helichryseæ. The Helichryseæ in America are limited to two genera, while there are about a dozen Eu-gnaphalieæ.

The separation of the Angianthiæ (Australian) from the Relhaniinæ and Athrixiinæ (South African) which was suggested in Chapter VI, C, is confirmed. The arrangement of the other sub-tribes is in accordance with the facts of distribution, especially the suggested origin of the Bupthalthminæ from the Inulinæ; both are Mediterranean with extension to South Africa and the latter sub-tribe has the wider area.

Cynareæ. The derivation of the Centaureinæ from the Bupthalthminæ is confirmed by the co-incidence of the centres of those two sub-tribes. The relatively primitive position of the Centaureinæ and Carduinæ is confirmed by the extension of these two groups into America, while the other two are limited to the Old World.

Mutisieæ. The derivation of the Nassauviinæ from the Senecioninæ is confirmed by the co-incidence of centres of concentration in these two groups. The primitive position of *Trixis* in the Nassauviinæ is confirmed by its comparatively wide area; the position of *Mutisia* and *Onoseris* as the basal genera of the Onoseridinæ (cp. Chaps. IV, F, and V, C-D) is confirmed by the wide South American distribution of these two genera. The distribution of the genera of the Onoseridinæ and Gochnatiinæ is also in accordance with their origin from *Mutisia*; *Chuquiragua* in South America and the *Ainslia-Dicoma* plexus in the Old World are indicated as the primitive genera of the Gochnatiinæ. The distribution of the Gerberinæ is in accordance with the origin of that sub-tribe from *Onoseris*; *Chaptalia* with a wide distribution connecting with *Gerbera* in the Old World forms the primitive plexus of the subtribe. The Barnadesiinæ are probably a group which has arisen independently of the rest of the Mutisieæ in the same place from the same source, but probably at a later date.

As the Mutisieæ develop chiefly in tropical and sub-tropical America and Africa, it is probably a result of their physiological

differentiation that present conditions make the Alaska-Siberian bridge impassable for this group. The probable use of the bridge before the last period of glaciation in the north is indicated by the distribution of *Gerbera* and *Trixis* (Fig. 35) and by the close affinity of the wider spread genera of both hemispheres in each of the sub-tribes which reach the Old World.

Vernoniae. The derivation of the Vernoniinæ from the Liabinæ is confirmed by the very close proximity, if not the actual co-incidence, of the centres of origin of these two sub-tribes (Figs. 30 & 36). The derivative position and relative youth of the Lychnophorinæ are confirmed by the smaller development of this sub-tribe in those regions where it occurs, and by the absence of any considerable development to compare with the tropical African concentration of the Vernoniinæ.

Astereæ. Various suggestions have been made for alterations in the positions of the sub-tribes in the Astereæ (see Chapter IV, D and Chapter V, D). The evidence of the distribution is also somewhat uncertain. The origin of the Homochrominæ from the Senecioninæ is confirmed by the co-incidence of the centre of origin of the former with a large concentration of the latter in Mexico and the U.S.A. The predominance in genera and species of the Homochrominæ over the Heterochrominæ in the region of origin supports the relative age of the former, while the wide distribution of the latter suggests that it is the group which has given most of the other sub-tribes.

The greatest development of the Baccharidinæ coincides with a considerable development of both the basal sub-tribes (Fig. 37), so that the evidence of structure decides the balance in favour of the Heterochrominæ as the source of that sub-tribe. The African development of the Conyzinæ and Grangeinæ confirms the origin of these sub-tribes from the Heterochrominæ as suggested (Chapter IV, D). The Mexican concentration and wide area of the Bellidinæ confirm the origin of this sub-tribe from the Homochrominæ, as suggested (Chap. V, D).

Eupatorieæ. The co-incidence of the chief centre of the Ageratinæ with one of the most important centres of the Heterochrominæ confirms the origin of the former sub-tribe as suggested in Chapter IV, F). The wider area of the Ageratinæ compared with that of the Adenostylinæ or Piqueriinæ and the co-incidence of all three centres in the Mexican region confirms the derivative position of those two sub-tribes. The exceptional

distribution of *Adenostemma viscosum* (Piqueriinæ) is clearly the result of its very effective means of dispersal (IV, 98.)

Heliantheæ. The wide areas of a number of genera in the Verbesininæ (Fig. 39) and the slightly less wide distribution of the Coreopsidinæ confirm the basal positions of those two groups. The Mexican centres and distribution of the Madiinæ, Zinniinæ and Lagasceinæ, and the Mexican-West Indian development of the Milleriinæ confirm the positions of these sub-tribes. The Chilian centre of the Petrobiinæ co-incides with a considerable development of the Verbesininæ. The position of *Petrobium* on St. Helena can only be accounted for by a polyphyletic origin of this sub-tribe: the probability of polyphylesis will be considered in the next chapter. The wide distribution in America of the Galinsoginæ and their diffuse development from the U.S.A. to the Andes confirms the direct origin of this group at a comparatively early date from the Verbesininæ.

Heleniææ. Except for their almost complete absence from the U.S.A. the Tagetinæ show a remarkable similarity in their distribution to that of the Galinsoginæ, so that the origin of the former from the latter sub-tribe is more or less confirmed, but the facts of distribution would also support an origin of the Tagetinæ from the Senecioninæ as suggested in Chapter V, D. The Mexican centres and areas occupied by the other sub-tribes are in accordance with their relationships, as suggested in Fig. 7 and modified in Chapter IV, D. The extension of *Jaumea* and other details of the distribution of the Jaumeinæ confirms the suggestion (Chapter IV, D) that this sub-tribe arose not later than the Baeriinæ. The independent origin of the Heleniinæ suggested in Fig. 7 and confirmed in Chapter III, E, is in accordance with its distribution, which is more like that of the Baeriinæ than that of the Tagetinæ.

Conclusions. It is clear, therefore, that (except for the derivation of the Conyzinæ from the Homochrominæ and the reversal of the positions of the sections of the Gnaphaliinæ) the views on the origin and development of the tribes of the Compositæ which have been given in Fig. 7 (Chapter II) and modified slightly in subsequent chapters receive complete confirmation in considerable detail from the study of the geographical distribution of the family.

The value of the graphic method of using maps for each genus or tribe, instead of the statistical method used by Bentham, is clearly proved.

The elucidation of the principle of physiological differentiation and restriction of area enables us to understand many peculiarities of distribution.

The usefulness and fundamental truth of the Law of Age and Area in its wider application to absolute age and total area are demonstrated with a considerable degree of certainty by the striking way in which the action of the law can be traced as agreeing with the phyletic conclusions based on the floral morphology and physiology of the family.

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CHAPTER XI.

THE ORIGIN OF THE COMPOSITÆ.

IN the previous chapters phylesis has been studied by the methods of comparative morphology, and a comparison of the details of the movements of the styles and stamens has been added. The conclusions arrived at have been tested by the geographical distribution of the groups (Chap. X). The phyletic data which have been elucidated would seem to support the origin of species by mutation and by the direct action of environment. Evidence is also given of the action of the Age and Area Law and, to a certain extent, the Differentiation Theory of Guppy is supported. It appears that Natural Selection has acted only on broad lines, such as the large development of Compositæ in the best situations for the dispersal of the fruits, and the selection of the mountain ranges as the path of migration.

In view of the multiplicity of evolutionary theories at the present time it is necessary to examine these and to endeavour to state precisely the evolutionary theory which appears to be most in accordance with the results of the present study before proceeding to any detailed enquiry on the actual origin of the family. The problem of this origin has four main facets—(1) From what group of plants did the family arise? (2) By what method? (3) In what region? (4) At what geological time? The first three points are discussed in the present chapter, the second being taken before the others in order to make the discussion of the first problem more circumscribed and precise. A brief summary of previous views on the origin of the family is given in the first section.

A. HISTORY.

Linné (I, 59, p. 415) classed *Dipsacus* and *Fasione* with the Compositæ in his "Communes" and later (I, 59, p. 441) he placed

Lobelia and *Jasione* in the Syngenesia. These suggested affinities cover the range of almost all subsequent views on the origin of the Compositæ. Allen (IV, 1) covers even a wider range when he writes of the "closely allied Dipsacæ, Valerianæ, Lobeliaceæ and Campanulaceæ."

The Dipsaceous origin is upheld by Bessey (I, 10) and by Bentham (I, 8), see Chap. I, B. The latter, although he classed the Compositæ with the Dipsacæ in the Asterales and was "unable to see any grounds for supposing, with Delpino, that the Lobeliæ are the parents of the Compositæ" (6, p. 8), gave the other view in his phylogenetic scheme (Chap. I, Fig. 2), where he follows Cassini (Chap. I, Fig. 1) in suggesting an affinity between the Cichoriæ and the Campanulaceæ through the Lobelioideæ.

The origin of the Compositæ from Lobelioideæ has been upheld by all other writers on the subject, beginning with Batsch (see Chap. I, B). Delpino (Chap. I, Tab. III), Höck (I, 41), Wernham (Chap. I, B), Hallier (21-22 and I, 38) and Engler (I, 30) are others who have expressed this view.

The present writer has suggested other points of affinity between the Compositæ and the Lobelioideæ (IV, 74, p. 198 and III, 49, p. 267), but the most detailed comparison yet made is by Kirchner (33). This author follows the development of the various genera of the Campanulaceæ into the Compositæ and a summary of the points which he finds to be common to the two groups may be useful. These are (1) protandry, (2) pollen presented on outside of style, (3) autogamy by curving of style, (4) capitula as in *Jasione* and *Phyteuma*, (5) syngenesy which is suggested in *Jasione* and accomplished in *Symphandra*, (6) nectar stored in the narrow, lower part of the corolla tube as in *Trachelium* and Compositæ, (7) nectary at the base of the style as in *Adenophora* and Compositæ.

No other family except those mentioned above has been seriously considered as the source of the Compositæ, and although some may show involucrate heads, syngenesy etc., these characters occur combined with numerous others which are quite different from those of the Compositæ, while the remarkable number of characters which are common to the Lobelioideæ and the Compositæ leaves very little doubt of the true affinity of the two groups.

B. THEORIES OF EVOLUTION.

Although the literature of evolution is extensive very few writers give a general account of modern theories, and none except

Bergson has yet attempted to expound a synthetic theory. This exposition by Bergson of evolution (7) is only partly scientific; it is rather metaphysical and transcendental as befits the work of a philosopher. It is, however, of the greatest importance to the student of evolution who desires to appreciate the true meaning of the development and progress of life.

Perhaps this brings the expression "life force" to the mind of the reader; if so it is necessary to point out that the original phrase "*un élan de la vie*" is translated by "vital impetus" or "impulse of life" and not by "life force." These phrases give a better idea of what Bergson means than the popular "life force" does (cp. 47).

According to Bergson (op. cit., p. 103) evolution "proceeds rather like a shell, which suddenly bursts into fragments, and these fragments, being themselves shells, burst in their turn into fragments destined to burst again, and so on for a time incommensurably long. We perceive only what is nearest to us, namely, the scattered movements of the pulverized explosions."

Other general accounts of less importance are given by Bernard (8) and the writer (47), and various aspects are treated by different authors in *Darwin and Modern Science* (45).

Natural Selection.

The theory of the origin of species by the elimination of all except the fittest of a series of infinitesimal variations (11, 16) has been widely accepted since 1858, but few recent experimentalists support this view, although not many deny it altogether.

One of the few supporters is Stout (50-51) but there is much in his work on *Cichorium* that requires revision. For example, he makes a strong point of the fact that the mode of the flower number *per head* in *Cichorium* does not fall in the Fibonacci series. The vast majority of the data refer to the ray florets (which are not present in *Cichorium*) and, as Church (IV, 18, p. 116) has shown, the Fibonacci series in the number of rays depends on the number of long spirals in the inflorescence and the sub-division of these spirals according to the 2 : 1 : 2 : 1 : 2 arrangement (see Chap. VIII). The number of spirals in the disc is definite and usually in the Fibonacci series but the number of flowers in each spiral is very indefinite (cp. IV, 18, p. 133). There is, therefore, no apparent reason why the total flower number *per head* should be in the Fibonacci series or discontinuous at all, although the discon-

tinuity in the number of ray florets and the occurrence of Fibonacci numbers among them is abundantly proved.

Willis (58-60, X, 74 and IV, 93) is one of the few who have in recent years written for the specific purpose of controverting natural selection but many have expressed doubts as to the causative action of such a negative principle as elimination. Walton (54) writing of the direct connection between the rotation of the earth and the rotation of aquatic micro-organisms says "Any attempt to account for it on the basis of natural selection can scarcely gain credence." The denial of the theory is also not uncommon among amateur naturalists who have spent many years in close observation of wild life. Thus Fountain (16), as a result of his observations on the celerity with which animals detect their prey in spite of so-called protective colouring, regards the whole theory of protective colouration as the result of insufficient observation in the field followed by inaccurate fireside reasoning, and pours scorn on the the natural selectionists in general (cp. op. cit., p. 95).

The elimination of the unfit by natural selection is a biological axiom which is not controverted by anyone, but its effect as an originating cause of species is not so evident.

Hybridisation

The most extreme views on the theory of the origin of species by hybridisation are expressed by Lotsy (35-36). This theory receives substantial support from the well-known and completely proved phenomena of Mendelism and from the work of Jeffrey and his collaborators (29, etc.). In spite of the extremeness of his views Lotsy has given definitions of "Linneon" and "Jordanon" (36) which should prove very useful if applied in future experimental work, since he distinguishes carefully between taxonomic species and genetically pure species.

It seems very clear from the Mendelian work that distinct forms or even species may arise by Mendelian segregation and recombination. The segregates of *Senecio vulgaris* obtained by Trow (IV, 84) would almost certainly have been described as separate species if they had been examined and described in the usual way by the usual taxonomists. Cockayne (X, 15) gives specific cases of confusion between hybrids and true species.

The cytological work of Morgan and others (38-39) has furnished a reasonable foundation in structure for the origin of very varied types by Mendelian segregation. The origin of new characters which is necessary for progress is not, however

explained by Mendelism (cp. 11). This difficulty is avoided by some Mendelians who claim that little or no progress but only loss of characters and diversification have taken place (cp. Bateson, 35, p. 89).

An interesting point is the variability of Mendelian factors or genes. That they are invariable is accepted more or less as an axiom by many Mendelians and the point was made precise by Johannsen (31) in the theory of pure lines or genotypes. Cockerell (IV, 19), who finds that a few genes or potentialities can give many varieties, concludes that new genes, though rare, do occur in the annual sunflowers. The variability of genes is upheld by Castle (12), and also by Stout (50) and Harris (23-24): the last two authors criticise Johannsen's work and the genotype theory very adversely, and this criticism is supported by the details of Jennings' work on *Paramœcium* (30 and Gates 35).

Mutations.

That mutations or discontinuous variations occur in the Compositæ is clear from the evidence which has already been mentioned (see Chap. IV, A). The truth of the phenomena described by De Vries (IV, 87-88) has never been denied, but Mendelians claim that all the phenomena can be explained by hybridisation and subsequent segregation, with occasional loss of genes (cp. 35).

White (56) claims priority for his observations (1898-99) of mutations in *Lycopersicum*. Cockayne (X, 15) makes a similar claim for Armstrong (1881). Davenport (14) mentions mutations which are sterile with the parent species (the accepted proof of specific differentiation). Willis throughout his work on Age and Area supports the views of De Vries, especially in his earlier papers (58-60, X, 74 and IV, 93) and in his special studies of the hill-top floras (IX, 43-45). The facts in the latter papers are supported by those given by Gibbs (X, 31).

Two interesting points are mass mutation and tetraploid mutation. The former is described by Bartlett (3-4) as the production of a large proportion (sometimes 100% of progeny) of mutants from certain parents. These mutants are themselves very unstable but do not throw off the type form of the species. This phenomenon is inexplicable by Mendelian segregation, but the loss of a factor giving a 100% mutant progeny is quite in accordance with Mendelian ideas. Mass mutation is also another possible reason for the occurrence on islands of endemic species of genera which are otherwise unrepresented in the same region (cp. Differentiation, Chap. X, A).

Tetraploid mutation giving pairs of species, one species usually larger in every way than the other, is described by Gates (IV, 32) who also gives a general account of the part played by mutation in evolution (18) and applies the conception very successfully and in considerable detail to special systematic groups (X, 28-29), thereby proving that the theory of mutation is distinctly useful in the study of the details of classification. The mutation in this case is frequently, if not always, to be interpreted as a result of hybridisation (see Chap. XII, B).

The occurrence of mutations in the Compositæ is either suggested or proved by many observations (see X, 59; VI, 15; IV, 8a, 40, 45, 66, 68, 82 and 84). Besides *Oenothera*, the Compositæ and the cases given by De Vries (IV, 87-88), there is *Capsella Hoeggeri* (49), *C. Viguieri* (9), *Juglans* (1), *Matthiola* (17), *Solanum* (26), *Gossypium*, (32), *Pleodorina* (20) and *Drosophila* (38). Few cases (cp. Lotsy, 35) of progressive mutations from a pure, homozygous stock have yet been thoroughly proved. Retrogressive mutation by the loss or suppression of a factor explains most, but not all, the cases which are inexplicable by segregation.

Orthogenesis.

According to Bergson, orthogenesis or "the continuity of direction of successive mutations" is due to the direction of the "élan originel de la vie," but somewhat less metaphysical ground is adopted by Wernham (I, 88, p. 136), who says that "Critical tendencies are no less important than critical characters," and also that "In the progeny . . . the characters are constant and completely evolved; and the line which unites ancestor and descendants represents the transition between tendencies and their realisation." To the student of Bergson the "tendency" is clearly the direction of the "becoming" and the fixity of the characters in the progeny is a lapse on the part of the author into the artificial, cinematographic point of view which is the normal attitude of the scientist,

The importance of orthogenesis in evolution is emphasised by Himmelbauer (X, 39) and Benedict (5). The facts given by the latter are very striking and his phrase "orthogenetic saltation" summarises very aptly in scientific phraseology Bergson's view of evolution as a combination of "*déroulement*" and "*déclanchement*," the unrolling being orthogenesis and the explosion resulting from the "*déclanchement*" being saltation or mutation (cp. 7, pp. 78 and 91).

Coulter (13) defines orthogenesis as "progressive evolution in a given direction, in contrast with the more or less successful variations in several directions involved in the theories of natural selection and mutation." He considers orthogenesis to be a response to evolution of climate (cp. X, 43, Chap. XXX), i.e. to "a persistent change in the conditions of living." This, as he points out, makes orthogenesis a physical rather than a vitalistic phenomenon and such a view explains most, if not all, orthogenetic development.

Throughout the *Compositæ* Coulter's explanation is satisfactory. Such cases as the tendency to dorsiventrality in the *Tristichaceæ* and *Podostemaceæ*, however, seem to require correlation in addition to epharmosis for their complete explanation. It is noteworthy also, that most lines of orthogenesis can be explained by loss of factors. All the cases of reduction or aggregation of parts, which form the chief examples of orthogenesis, are clearly retrogressive mutations, e.g. the keynote of the evolution of green plants is generally recognised to be the progressive sterilisation of potentially reproductive cells.

Epharmosis

In its original sense, as used by Vesque (53) epharmosis is distinguished from adaptation; adaptation is described as the effect of epharmosis after the effect has been transmitted by heredity and fixed by selection (op. cit., p. 44), but it is proposed to use the term epharmosis here as meaning the act of developing epharmony in Cockayne's sense of the word (see above, *Action of Environment*, Chap. X, A). This limits epharmony to adaptations which are the direct result of an environmental stimulus and excludes such changes as may be due to mutations or other spontaneous variations, and which may happen to be advantageous, while at the same time it removes the distinction between fixed and unfixed variations. There is as yet no direct evidence either for or against the fixation of epharmonic characters, but there are a large number of facts, which can be used to prove the probability of such fixation in plants.

The powerful effect of environment in producing advantageous modifications of structure or physiological behaviour is implicit in much of the theorising on the origin of land plants. It is very significant also that Sargent, Hill, and Henslow, with three different theories, all attribute the origin of monocotyledony to an action of environment, which in all three cases is more or less direct (see

Bancroft, 2, and Sinnott, 46, p. 566). Jordan apparently had some idea of epharmosis when he wrote (X, 44, p. 17) "Si l'on entend que la sélection naturelle ou sélection inconsciente de la nature, comme disent Darwinistes, s'opère indépendamment des causes extérieures il suffira de faire remarquer que cette sélection n'existe pas."

It is noteworthy that ecologists and most botanists who have made a careful study of plants in the field are among the chief supporters of the causative action of epharmosis in the origin of species. Spruce (X, 69, Vol. II, p. 357) says "Of the riparial plants, nearly every species has its congener on terra firma, to which it stands so near that, although the two must of right bear different names, the differences of structure are precisely such as might have been brought about by long exposure even to the existing state of things, without supposing them to date from widely different conditions in the remote past." Warming (X, 71, Chap. 100) gives a summary of various aspects of epharmosis, a term which he uses for self-regulation or direct adaptation, implying in his expression "they directly adapt themselves" a metaphysical view of evolution closely akin to that of Bergson. The definition given above in accordance with Cockayne's view does not imply any teleological action.

Warming gives many references, one of the most important being Goebel (19). Some of the points he mentions may be applied to the Compositæ—(1) illumination altering leaf-position, *e.g.* the compass-plants, *Lactuca Scariola* and *Silphium laciniatum*; (2) aerial and subterranean conditions as affecting external structure, *e.g.* various Compositæ (X, 19); (3) epharmonic xeromorphy, *e.g.* various Compositæ (see 41 and X, 6, 16, 36, 48, 51, 56, 60 and 63); (4) hydrophytes: the changing of *Polygonum amphibium* in a few weeks from the land-form to the aquatic form is paralleled by the even more striking case of *Cnicus arvensis* (X, 18, and Chap. X, A), (5) changes in food-supply inducing distinctions in floral structure, *e.g.* *Dimorphotheca pluvialis* (Chap. IV, C); (6) internal structure as affected by external conditions, *e.g.* *Raoulia*, *Senecio*, etc. (X, 26 etc.); (7) plasticity of biological characters, *e.g.* action of climate on irritability (see Chap. III, especially *Torenia* and notes 14, 15, 18, 31 and 33); (8) specially marked plasticity and genera in a condition of active evolution, *e.g.* *Hieracium* (II, 55).

Warming (loc. cit.) mentions that epharmosis is more or less confined to the vegetative organs and to the metabolism of the plant. "The flowering shoot in its development follows laws

that, in some ways, differ entirely from those concerning vegetative organs." The effect of food and light on the corolla in the Compositæ has already been noted (cp. *Helianthus*, V, 21 and Chap. IV), and that external conditions may have a marked effect even on the inflorescence in the Compositæ is shown by the production of a solitary capitulum, instead of a compound inflorescence, in *Rudbeckia* under adverse conditions (IV, 44), by the seasonal variation in the number of ray and disc florets described by Nakano (VIII, 19) and others, and also by the floral changes produced by injury (IV, 23), grafting (IV, 24) and parasites (IV, 55-56a). That the modifications caused by the environment in such details are of taxonomic importance is shown by the fact that hairs may be diagnostic characters, e.g. in *Senecio* (25); many of the other characters are also used in diagnostic keys to the species.

The permanence in heredity of epharmonic variations is accepted by Warming as proved, but more detailed evidence on this point is given by Henslow (27 and X, 38). Cockayne (X, 15, p. 13) cites quite a number of workers who have given reasons for their adherence to this neo-Lamarckian doctrine. Even Weismann was "driven to the conclusion that the ultimate origin of hereditary individual differences lies in the direct action of external influences upon the organism" (55, p. 279 and cp. Macbride, 35). Whether such inheritance of acquired characters is true or not for the species or genotypes (Jordanons, etc.) as defined by the Mendelians, it seems certain that many *taxonomic* species (which are based on morphological structure and which have not been examined genetically) are the result of the direct action of the environment.

The remarkable plasticity of the Compositæ is apparent throughout most of the work on epharmosis. For example, the Compositæ give more than one-seventh of the species in New Zealand (X, 93, p. 278), but this does not altogether account for the fact that Cockayne draws examples from the family for every one of his sections on response to ecological factors (X, 15, pp. 15 sqq.); soil—*Cotula Haastii*, *C. Featherstonii*, *Senecio antipodus*; light—*Olearia insignis*; wind—*Olearia ilicifolia*; water—*Cotula coronopifolia*; altitude—*Celmisia argentea*; as well as for the after-effect of stimuli—*Olearia Lyalli*, *O. Colensoi*; for convergent epharmony—*Celmisia*, *Haastia*, *Psychrophyton*, and for persistent juvenile forms—*Helichrysum*,

The most recent example has been worked out by Wall (53a),

who has shown that two New Zealand species of *Senecio*, *S. saxifragoides* and *S. lagopus*, are microspecies of the same aggregate. They are distinguished only by the sparseness or abundance of the bristle-like, glandular hairs on the leaves. "Those differences in degree, being certainly hereditary, constitute true unit characters." It is further suggested that the difference is "of climatic origin" and that "the drier climate of the Port Hills has directly determined the development of *S. saxifragoides*."

Other papers of interest in connection with epharmosis are by Harshberger (X, 35), Raunkiaer (45), Poole (42), Bonnier (X, 8-9), Cockayne and Foweraker (X, 17), Dauphiné (X, 22), Foweraker (X, 26), Gates (X, 27), Harris (X, 33), Oger (X, 56), Schröter and Hauri (X, 60), Shreve (X, 63-64), Sinnott and Bailey (46 and X, 5), Massart (X, 53), and Bames (15). For further literature the reader is referred to Goebel (19), Warming (X, 71), Henslow (X, 38), Cockayne (X, 15-17), Schimper (IX 32) and De Vries (IV, 87, pp. 438 seq.).

Isolation and Differentiation.

A. Jordan's theory of the origin of species by isolation was revived by D. S. Jordan (X, 45) and is expressed thus. "Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighbouring district separated from the first by a barrier of some sort." This is shown to be true for *Eriodictyon* by Abrams and Smiley (X, 1) and the idea is applied by some taxonomists, when they raise geographical forms to specific rank (cp. 37). It is not, however, recognised as a general truth in the plant kingdom, for as Lloyd (X, 47) points out, the more general phenomenon is the occurrence of the most closely related species in the same region. Cockayne (X, 15) gives a number of specific instances of the occurrence of closely related species side by side in the same region and quotes Leavitt (34), who considers this phenomenon to be evidence in support of the action of mutation rather than that of natural selection or epharmosis. "Mutation breaks the species, and momentarily at least must give a polytypic aspect to the group within a specific area" (*loc. cit.* p. 211).

The theory of "the differentiation of primitive world-ranging types in response to the differentiation of their conditions" Guppy, IX, 22, p. 313) has already been mentioned (Chap. X, A)

and is closely akin to the action of isolation and epharmosis. Of these theories which attempt to explain more or less the same phenomena, epharmosis is supported by the most conclusive evidence. Even Andrews (X, 3-4), who is quoted by Guppy in support of his theory writes (X, 4, p. 536) of "an organic response to severer conditions of climate and to a greater poverty and porosity of soil."

Fountain's opinion is interesting as that of an amateur, who knew little of botany and less of the literature of epharmosis. He writes (16, p. 227) "In fact, the peccary, as all, or nearly all, other animals bears out my theory that species (that is variations from *original types*) are the outcome of locality, and not of 'natural' or any other kind of 'selection.'"

Conclusions.

The action of orthogenetic saltation is discussed by Davenport (IV, 25), whose chief point is that internal laws give a breaking up of the complex germ plasm. He gives the origin of radium as an analogy but does not develop the analogy in the detail which it deserves.

Considering the "evolution" of the Uranium-Actinium Series (Fig. 41),¹ it will be noticed that, whereas some of the elements (to be regarded as species) have a long life, others are very unstable and exist only for a short time. Orthogenesis finds its analogue in the straight series from Uranium I to Radium C (Fig. 41) and from Thorium to Thorium C (Fig. 42), each step in the series being dependent on the preceding steps. Divergence of types finds its analogue in the splitting of Radium C (Fig. 41) and of Thorium C (Fig. 42) to give two distinct series each. The irreversibility of evolution (cf. 41a) is the same as that of the disintegration series.

Both infinitesimal variation and mutation have analogues, the former in those cases where the imponderable particle is thrown off, giving a new form and the latter in those cases where a perceptible explosion takes place and the helium particle is thrown off. It will be noticed that it is always by *loss* of something that a "mutant" arises. It is perhaps stretching the analogy too far to extend it to cytology, the first case corresponding to the loss of one gene from a chromosome and the second to the observed loss

¹ I am indebted to Dr. J. F. Spencer for the details given in Figs. 41-42. The times given are half life-periods, or the time taken for 50% of any given quantity of an element to change into the next of the series. The numbers within the circles are the atomic weights. The β particle is imponderable and the α particle (helium) has an atomic weight of 4. The dotted lines indicate probable but unconfirmed lines of development.

of a complete chromosome from the nucleus (cp. Gates on *Oenothera* mut. *lata* and mut. *gigas*, 18), but the suggestion may be useful.

The rapidity with which some of the elements break up to form the next of the series is analogous to the unstable mutants which De Vries suggests may intervene between successive stable forms, and which are said to be specially noticeable when mass mutation takes place (3). The analogous changes in the plant might take place either during nuclear division or in successive generations; the former case might well lead to the very marked mutations which are supposed by Willis (IV, 93) to occur, since the different stages in the disintegration of the parent would not be identified with corresponding external stages.

Polyphyly of genera or even of species, which is becoming

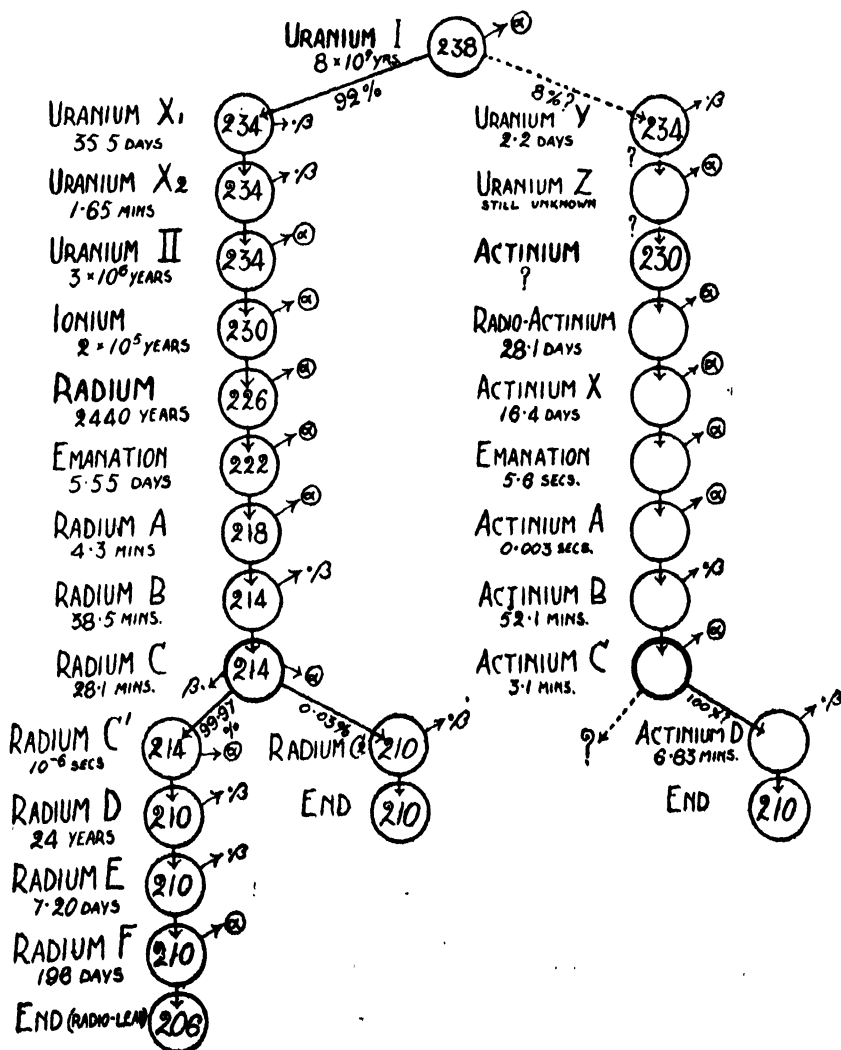


FIG. 41. Uranium-Actinium Disintegration Series.

generally recognised as not uncommon (cp. 10 and 40), and convergence, epharmonic or otherwise, which is also becoming recognised as an important point in evolution (cp. 10, 57 and X, 15 and X, 69, Vol. II, p. 115) have analogues here also. Convergence may be noted in Radium F and the end-products of the Radium C² and Actinium D lines, and also in the similarity of the end-products of all the disintegration series in both Figs. 41 and 42. Parallel evolution and polyphyly may be noted in the identity of the end-products of the last two lines in Fig. 41 and and of the Thorium C¹ and Thorium D lines (Fig. 42). Allotropic modifications, such as occur in sulphur, are unknown in the radio-active elements so that there is no analogy here for tetraploid mutations, although these find their analogue amongst the other elements.

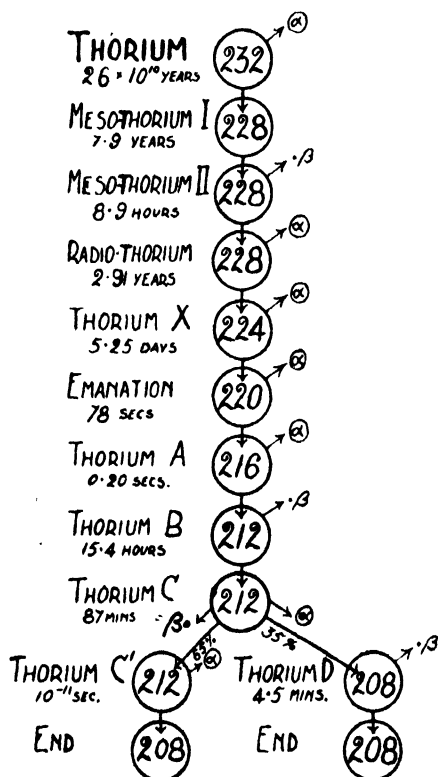


FIG. 42. Thorium Disintegration Series.

The radio-active analogy holds good, therefore, for most of the details of orthogenetic saltation; it fails, however, to be complete for evolution because external circumstances have apparently no effect on the course of the disintegration and the form of the constituent members of the uranium and thorium series. This is more or less true for orthogenetic saltation alone but epharmosis finds no analogue in radio-activity. Such an analogue does, however, occur in crystallisation and other chemical phenomena which simulate the processes of life.

"The truth is that adaptation explains the sinuosities of the movement of evolution, but not its general directions, still less the movement itself." (Bergson, op. cit., p. 107). Elsewhere this philosopher compares life and evolution to a river—"The movement of the stream is distinct from the river bed, although it must adopt its winding course," (op. cit., p. 284). Dendy (35) uses the

analogy of a piece of music with its main theme and the variations but applies it in rather a different way. He agrees with Bergson, however, in regarding evolution as a dual process. That the analogy of a stream cannot be followed without reserve is clear from the passage quoted at the beginning of Section B and from another which emphasises the part played by contingency in evolution; "Two things only are necessary: (1) a gradual accumulation of energy; (2) an elastic canalization of this energy in variable and indeterminable directions, at the end of which are free acts."

If we place a number of water-falls and anastomosing back-waters at intervals along the metaphorical stream, we get some approach to the "explosions" and "free acts". Bergson's view of evolution can then be translated into scientific phraseology thus—the smooth flowing stretches of the "stream" correspond to orthogenetic development; the water-falls, explosions or free acts are saltations which give rise to the branches or back-waters of the stream; the river bed with its sinuosities is the environment, which by epharmosis and elimination of the unfit keeps the stream within definite limits. In this way we get a synthetic, eclectic theory of evolution which includes all the diverse points of view and assigns to them their proper place in the complete scheme.

In evolution by *orthogenetic saltation*¹, with *epharmosis* and *elimination of the unfit* exercising a directing and delimiting function on the actual forms assumed by organised life², we have the best of Darwinism, neo-Lamarckism, neo-vitalism, Mendelism and the mutation theory.

Something of this kind, but without the precision rendered possible by recent work is foreshadowed by Bentham (cp. quotation,

¹ Orthogenetic saltation may decide the inner constitution of a species, but the expression of that constitution is modified by epharmosis. Probably the inner constitution, as well as its expression in the form and structure of the plant, is altered by the cumulative effect of continued epharmonic adaptation. The saltation may be either Mendelian or De Vriesian or both, Mendelian segregation having most evidence to support it as an originating cause of a large number of *taxonomic* species or even genera (cp. Rendle, 35). Progressive mutations seem to be as rare as the proved origin of new genes, but their rarity is quite in accordance with their place in the general scheme of evolution, as will be readily evident to anyone who tries to solve the Biochronic Equation of any highly organised species (see IV, 88, p. 674). It is remarkable how few characters which are not epharmonic are present in such a species and absent in others of lower systematic position.

² It is certain at least that epharmosis and, to a lesser degree, natural selection, decide the habit and many of the details of the structure of a species, even if the genetic constitution remains the same throughout a series of variations, a supposition which is, to say the least, unsupported by the necessary detailed evidence.

Chap. X, A), and by De Candolle (LX, 11, p. 1119), where after discussing the origin of species from one individual or from many individuals he writes "J'insiste sur ces doubles explications."

C. THE LOBELIOIDÆ.

If the theory of evolution by orthogenetic saltation and epharmosis is sound, we should find the chief characters of the Compositæ foreshadowed in the ancestral group.

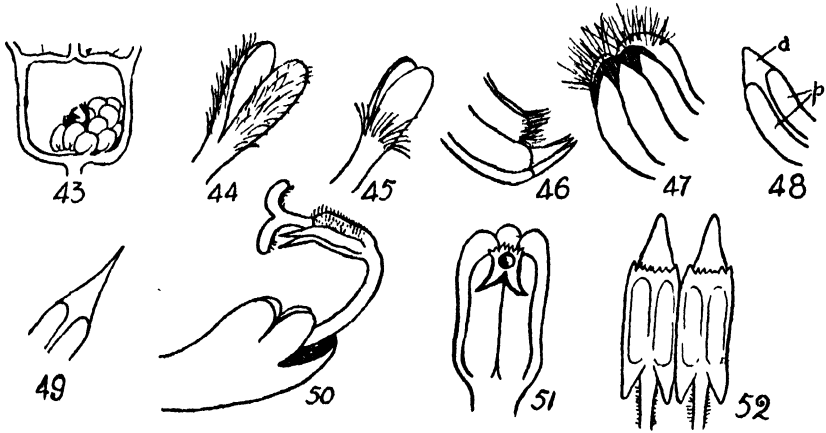
The general characteristics of the Lobelioideæ as given by Schönland (44) are the following:—Flowers usually distinctly zygomorphic, in a few cases unisexual; almost without exception pentamerous; calyx regular or bilabiate; corolla usually tubular, often slit down one side, rarely with the petals quite free; stamens usually more or less fused with each other and sometimes with the corolla also; anthers always syngenesious, usually with hairs or bristles at the apex; three anthers usually larger than the other two; style with a ring of hairs; ovary usually bilocular; fruit a berry or capsule, usually loculicidal at the apex, more seldom dehiscing laterally; herbs, shrubs or trees.

Gynœcium.—To begin with the gynœcium, the ovary is inferior or semi-inferior and bi-carpellary and the ovules are anatropous, all as in the Compositæ except the occasional semi-inferior ovary. Although the ovary is usually bilocular with axile placentation, the partition is incomplete in *Rhizocephalum* and absent altogether in *Apetahia* which has numerous ovules on parietal placentæ. A further stage is reached in *Lysipomia* where one loculus aborts and the ovules are few, grouped together on a more or less basal placenta (Fig. 43). If this is compared with the occasional occurrence of more than one ovule in the Compositæ (cp. Don, Chap. II, A, and 182), especially with the case of a bilocular, bi-ovulate ovary in *Senecio vulgaris* (1,82), it will be clear that in this character there is a tendency in the Lobelioideæ towards the condition in the Compositæ.

The style in the Lobelioideæ has sweeping-hairs on the outside; these may be in a ring, as in *Siphocampylus asper* (Fig. 45) or scattered as in *Lysipomia muscoides* (Fig. 44). This should be compared with the types in the Compositæ (Chap. II, Fig. 5). The two style branches are usually shorter than in the Compositæ, but they act as pollen-presenters in exactly the same way, even to the coiling back on themselves to give self-pollination.

Andræcium.—The syngenesy of the anthers is a well-known

feature of the Lobelioideæ but the appendages are of scarcely less importance in view of the great significance of these structures in the Compositæ. Apical appendages are present in most genera. In *Siphocampylus* some of the anthers have rigid, horny or membranous elongations of the connective, and the others have a tuft of hairs at the apex. There may be three teeth as in *S. psilophyllus*, *S. asper* (Fig. 46) and *S. lantanifolius* (Figs. 47-48), or only two as in *S. aggregatus* (Fig. 50). The lateral anthers in *S. lantanifolius* have the appendages very slightly developed but it is quite clear in the median anther (Fig. 48). The appendages may be obtuse or acute (cp. Figs. 48, 49 and 52). There are two teeth in *Lobelia corymbosa* (Fig. 51), *Pratia macrodon* (Fig. 52) and *Rhizocephalum*, and three in *Laurentia repens*.



FIGS. 43-52. Floral details of the Lobelioideæ.

FIG. 43. *Lysipomia muscoides*, ovary; 44, ditto, style; 45, *Siphocampylus asper*, style; 46, ditto, apical part of anther tube; 47, *S. lantanifolius*, apical part of anther tube; 48, ditto, median anther to show (a) appendage, and (p) pollen sacs; 49, *Laurentia repens*, apical appendage of anther, 50, *Siphocampylus aggregatus*, style and stamens to show apical appendages, 51, *Lobelia corymbosa*, anther tube to show apical appendages; 52, *Pratia macrodon*, two of the five appendaged stamens

All five anthers may have hairy appendages and be more or less equal, as in *Monopsis* and *Brighamia*; or the two smaller anthers only may be hairy, as in *Clermontia*, *Delissea*, *Sclerotheca* and *Hovellia*; or the condition may vary in the genus; all or only the two smaller anthers have hairy appendages in *Cyanea* and *Lysipomia*, or the appendages of these two anthers may be teeth or hairs, the other three being naked as in *Pratia* and *Isotoma*; while in *Centropogon* one section has the two smaller anthers with teeth, another has them with hairs and the third has all five anthers with no appendages at all. *Lobelia* shows a variation similar to that in *Centropogon*. In *Hypsela* there may be one tooth or a few bristles at the apex of the two smaller anthers,

Another point to be noticed is the incipient basal appendages in *Pratia macrodon* (Fig. 52), which are specially interesting as they occur where the filaments are free, a rather unusual condition in the Lobelioideæ, where the filaments are usually fused to form a tube.

The frequent occurrence of apical appendages and the rare occurrence of basal appendages to the anthers in the Lobelioideæ compare well with the prevalence in the Compositæ of the former and the gradual development of the latter from a type in which they are absent. That the biological significance of the apical appendages is the same as in the Compositæ is obvious when the more or less horizontal position of the anther tube is noted together with the position of the appendages (cp. Figs. 46, 47, 50 and 51). In the cases such as *Lysipomia muscoides*, where all the anthers are equally appendaged, the anther tube is usually, if not always, erect.

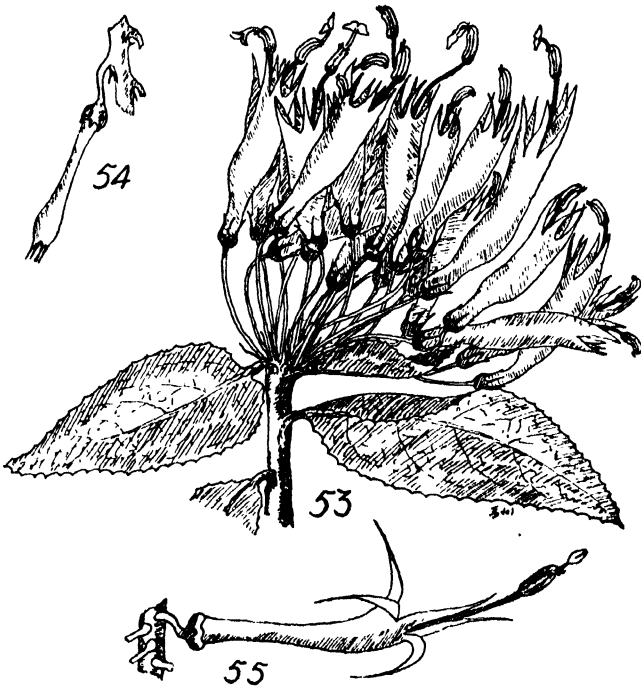
Irritability of the style or stamens has not yet been observed with certainty (cp. III, 49, p. 267), but in *Lobelia thapsoides* and *L. cardinalis* a very slight touch on the filaments or anther tube is sufficient to produce the presentation of a small quantity of pollen. It has not yet been ascertained whether this is due to a contraction of the filaments, which are united into a tube, or to the delicate adjustment of the style with its sweeping hairs inside the anther tube. Observations on this point in the natural habitats of the species would be of interest (cp. *Torenia*, Chap. III, B).

Corolla. Although typically bilabiate or irregular, the corolla is not infrequently almost or quite radially symmetric, as in some species of *Centropogon*, *Siphocampylus* (Figs 53-55), *Dialypetalum*, *Laurentia*, *Hypsela*, *Lysipomia*, *Rhizocephalum*, *Isotoma*, *Brighamia*, and *Downingia*. Indeed, there is a general tendency for the corolla to become more or less radially symmetric whenever the flowers become crowded or reduced in size (cp. Fig. 54 and *Dialypetalum*).

The colours of the corolla are usually of the higher types, blue red or purple, but orange and yellow occur in some species of *Siphocampylus*, *Centropogon*, *Heterotoma* and *Downingia*.

Calyx. The progressive reduction of the free lobes of the calyx from more or less foliose structures to mere undulations at the top of the receptacle is illustrated in the genus *Siphocampylus* (Figs. 53-55). The other genera show even more foliaceous sepals as a rule, but reduction is comparatively common; the extreme condition, as in Fig. 55, is reached in several genera.

Inflorescence. Solitary axillary flowers occur in a number of genera; simple and corymbose racemes are common. The tendency of the corymb to form a racemose umbel develops in various species of *Siphocampylus*, including *lantaniifolius* (Fig. 53), *microstoma*, *corymbiferus*, *gracilis*, *aggregatus*, and *reticulatus*, and also in *Jasione* and *Phyteuma* of the Campanuloideæ (cp. also *Campanula glomerata*). A dense, short corymb which is a close approach to a capitulum occurs in *Lobelia corymbosa*. The inflorescence of *Centropogon densiflorus* varies from a short raceme almost to a racemose umbel, and the more umbellate it is the more flowers are ebracteolate. This occurs in a number of other species of the genus.



FIGS. 53-55. Inflorescence etc. of *Siphocampylus*.

FIG. 53, *S. lantaniifolius*, complete inflorescence; 54, *S. asper*, portion of raceme; 55, *S. eximus*, portion of raceme (after Planchon).

Bracts. The general tendency throughout the tribe is the same as in *Centropogon*: the closer the inflorescence approaches an umbel the fewer and more reduced are the inner bracts. This reduction of the bracts in *Siphocampylus* is more or less correlated with the reduction of the calyx (cp. Figs. 53-55). Even in the simple racemes there is a tendency for the upper bracts to disappear, as in *S. angustifolius* and *S. flagelliformis*.

Involucre. In the cases where the inner or upper bracts are reduced or even completely absent, the outer or lower bracts usually remain more or less foliaceous (cp. Fig. 53), although they

may be reduced to a certain extent. *Siphocampylus reticulatus*, for instance, shows in some specimens an inflorescence which might almost be described as an involucrate umbel. *S. corymbiferus* also shows a very close approach to a capitulum, but the inner bracts and the calyx are only moderately reduced (see also *Lysipomia acaulis*, X, 72, p. 198). In the Campanuloideæ the involucre is diffuse in *Phyteuma*, uniseriate in *P. comosum*, biseriate in *Hedraeanthus tenuifolius* and multiseriate in *Yasione*.

Habit. A very good account of this subject is given by Bentham (6). The more widespread types are herbaceous, perennials or annuals, as in the Compositæ, and, as in that family and many others, the insular species are more or less woody. As in the Compositæ also, the scrambling climbers are most abundant in open scrub and around the edges of the tropical forests, especially in South America. Erect woody forms occur at high altitudes, especially in the Andes, where the ericoid, abietoid and lycopodioid forms are very interesting. Similar forms occur in the Compositæ, (see Chap. X and Weberbauer, X, 72, Fig. 26, C and F, Goebel, X, 32, Pl., VIII, Figs. 2a-2b and Schimper, IX, 32, Fig. 409). The perennial herbs develop large, coarse plants with a racemose inflorescence in some regions and the erect Lobeliæ of Africa may be compared with the Ligulariæ of Asia. It remains to note that the leaves are usually alternate.

Latex. The occurrence of laticiferous vessels in the Lobelioideæ is also of interest. Our knowledge of these structures in the Lobelioideæ is by no means complete, and the absence of latex in the species of *Rhizocephalum* and a few other genera which have been examined is significant. Latex is present in some species of *Siphocampylus*, *Centropogon* and many other genera; *Lysipomia* does not seem to have been examined (see Chap. XII, C).

Summarising the points in which the Lobelioideæ show characters and tendencies, or lines of orthogenesis, leading towards the Compositæ we have—

1. Inferior or semi-inferior ovary with anatropous ovules.
2. Reduction of the quinquelocular ovary of the lower Campanuloideæ to a bilocular ovary and finally to a few ovules on more or less basal placenta.
3. Bifid style with collecting hairs; scattered or in a ring, and recurving of style branches to give ultimately self-pollination.
4. Pollen-presentation mechanism, protandrous and the same in principle, with the nectary at the base of the style and a suggestion of irritability of the stamens.

5. Syngenesious anthers, stamens sometimes epipetalous.
6. Prevalence and varying development of apical appendages to anthers.
7. Slight development of basal appendages to the anthers.
8. Actinomorphy of corolla in lower Campanulaceæ, zygomorphy with a return to actinomorphy, especially under conditions of reduced food supply (cp. Causal Morphology, Chap. IV, C) in the Lobelioideæ.
9. Variation in colour of corolla from yellowish-green to yellow, white, orange, purple, etc.
10. Reduction of calyx limb under crowded conditions of the flowers, progressing to complete absent of free lobes.
11. Progressive aggregation of the flowers with consequent reduction in corolla and calyx, together with the progressive disappearance of the inner or upper bracts of the racemose umbel.
12. Development of an involucre, diffuse in the Lobelioideæ but completely organised in certain special Campanuloideæ.
13. Alternate arrangement of leaves.
14. Laticiferous vessels present or not (see Chap. XII, C).
15. General habit and range of variation in habit.
16. Haustorial antipodal cells and prominent integumentary epithelium of embryo sac (see Chap. XII, B).

D. THE ORIGIN OF *Senecio*.

The above summary of the lines of orthogenesis in the Lobelioideæ is in complete accord with the basal position of *Senecio*. The floral characters would apply to the whole family more or less, but the complete disappearance of the free calyx limb affords additional evidence in support of the secondary nature of the pappus (cp. Chap. V and Chap. XII, D). The occurrence of the racemose umbel as a form of condensed inflorescence is in accordance with the view expressed on the origin of the capitulum (Chap. VI, B). The complete disappearance of the inner bracts is in accordance with the primitively naked condition of the receptacle and the atavistic nature of the receptacular paleæ (Chap. VII). The diffuse, slightly developed condition of the involucre in the umbellate Lobelioideæ is in accordance with the view expressed on the primitively uniseriate pericline with a slightly developed calyculus (Chap. VI). The alternate phyllotaxis of the leaves is in accordance with the view expressed on the primitive phyllotaxis in the Compositæ (Chap. VIII).

The range of habit is the same as in the Compositæ as a

whole but *Siphocampylus* shows a number of herbs with the common *Senecio* habit, while a number of the arborescent species of that genus are very similar in general appearance to some arborescent species of *Senecio*. We may also mention *Isotoma senecioides* (see 44, p. 66) with the habit of a weedy *Senecio*.

The final test, that of geographical distribution, may now be applied. In the Lobelioideæ there are six genera endemic in the Sandwich Islands, one in the Company Islands, and one in Madagascar. Of the other local genera one is Mexican, one extends from Abyssinia to South Africa, another from South Africa to Australia and three, *Lysipomia*, *Hypsela* and *Rhizocephalum*, are Andine. *Isotoma* has six species in Australia and one each in the West Indies and the Company Islands; *Laurentia* extends from North America to the Mediterranean and South Africa, and *Lobelia* is widespread, occurring in the Old World and in South America.

The genera which show the best development of anther appendages, aggregation of the flowers, etc. are the three Andine genera and the remaining widespread genera. These are *Pratia*, which extends from South America to Australia and tropical Asia, *Downingia*, which extends from Oregon and California to Chili, *Centropogon* and *Siphocampylus*, both of which extend from tropical South America to Central America and the West Indies. These last two genera have about 100 species each and show many of the above-mentioned tendencies. It should now be clear why the north of South America was taken in Chap. X as the centre of origin for *Senecio*,

I will now try to help the student to visualise the origin of the first *Senecio* as a living, moving process—in fact attempt the kind of presentation which has already been advocated in this journal. This attempt being necessarily descriptive cannot be other than cinematographical, but with a little mental effort and a little study of Bergson (7, pp. 314—330) the student may be able to perceive the “becoming” from *Siphocampylus* to *Senecio*. It will be sufficient to say that the following is an attempt to present the origin of one definite kind of living organism from another definite kind of living organism as a normal, natural result of the actual *living* of the parent organism in a particular region.

Let us suppose a certain species of *Siphocampylus* grows as an arborescent scrambler on the edge of the forest about the sources of the Amazons. It has already developed a racemose umbel as an inflorescence, the outer bracts remain more or less foliaceous,

while the inner bracts and the calyx limb are much reduced. The corolla is yellow in colour and zygomorphic. The stamens have the usual syngenesious anthers unequally appendaged. The ovary is bilocular with numerous ovules on axile placentæ.

As the years pass the species spreads (cp. Age and Area, Chap. X, A) until it reaches the zone, about 5000 ft. up on the slopes of the Andes, where the forest gives way to open scrub and grassland. Under the influence of the unfavourable conditions, (dryness, high winds, alternation of extreme temperatures,) the individual plants which become established in this region are stunted in growth and instead of scrambling over bushes become dwarf, trailing shrubs.

In this form the species extends to higher altitudes where true alpenes grow among the dwarfed, shrubby forms of species which are characteristic of the lower zone (cp. X, 69, Vol. II, p. 264). Under the more arid conditions the individuals which become established there are still more dwarfed. Coincident with the dwarfing of the individual, the reduction of the food supply causes the flowers to be smaller, the pedicels to be shorter (cp. *Lysipomia acaulis*, X, 72, p. 198), and the inner bracts and free calyx segments to disappear completely. This reduction enables the pressure of orthogenesis (as represented possibly by the climatic conditions) to crowd the flowers still closer (cp. I, 81, p. 30 and Chap. IV, B) and the corolla as a consequence becomes actinomorphic. The stamens as a result of correlation cease to be unequally developed, the anther tube becomes erect, the tooth-like appendages become equally developed on all the anthers (cp. *Lysipomia muscoides*). As a result of the reduced food-supply only a few ovules are developed near the base of the ovary and the septum aborts (cp. *Rhizocephalum* and *Lysipomia*).

Continued existence under these unfavourable conditions of excessive insolation, alternating with intense cold and combined with growth on the arid, wind-swept mountain slopes, would produce crowding of all parts of the plant to give a rosette or ericoid form (cp. alpine *Senecio Jacoben*, Chap. X, A, also IX, 32, pp. 704—716 and X, 72, numerous figures). These epharmonic variations would include the complete disappearance of the pedicels, the formation of a properly protective, uniseriate pericline, an indefinite calyculus, and a head of small flowers (cp. the close aggregation of the capitula and formation of secondary involucres in alpine Composites), and also the development of only one ovule in each indehiscent ovary for the further protection of the seed. The

development of the hairs on the fruit into the pappus mechanism may be a fortunate accident or an epharmonic variation; there is no clear evidence on this point at present. Thus we arrive at a plant with all the essential characters of a *Senecio*.

It must be noted that we started with a *Siphocampylus* with characters and tendencies which are known to be present in the genus, and we have appealed only to those orthogenetic lines or critical tendencies and to the direct influence of the external conditions to effect the change from a species of the Lobelioideæ to a species of the primitive genus of the Compositæ. The orthogenetic saltation in almost every detail involves the loss or suppression of a character and presumably of a factor. This is in accordance with Bateson's view of mutation (35). The progressive development of appendages to the stamens, may also be due to loss, if the view given in Chap. II of the origin of the appendages by the sterilisation of potentially sporogenous tissue is correct. The steps in the change from one genus to the other are natural and occur in related forms in the same region. Indeed, there is a distinct possibility that even at the present time a close examination of the variation of the species of the Lobelioideæ and *Senecio* in the critical region from the edge of the Matto Grosso to the *puna* of the Sierra would show the actual occurrence of forms such as have been suggested. These forms have already been observed in closely related genera in that particular region.

In any case, from the strictly scientific point of view a close affinity can be traced between the Lobelioideæ of the Andes and *Senecio*. So close is the affinity that we may be permitted to suggest a doubt as to the truth, in the case of the Compositæ, of the dictum of De Vries which is quoted by Horne (28) that "the great lines of evolution of whole families and even of genera..... obviously lie outside the limits of experimental observation."

The first three questions given in Section A of this chapter have been answered. The fourth—"at what geological time did the Compositæ arise?"—is considered in Section A of the following chapter.

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CHAPTER XII.

MISCELLANEOUS TOPICS.

THE preceding chapters have each dealt as far as possible with only one aspect of the origin and development of the Compositæ. There remain to be considered some subsidiary aspects, such as the palæobotany, cytology, laticiferous and secretory systems, seedling structure, etc. These are dealt with in the present chapter.

A. FOSSIL COMPOSITÆ.

An extensive but not quite exhaustive search through the literature of tertiary fossil plants has yielded the records for Compositæ given in Tables XII and XIII. The localities and geological dates are given in Table XII. The numbers in the second column of Table XIII refer to the bibliographical references given at the end of this chapter; with one or two exceptions the reference to the original description is given and comes first. The numbers in the third column of Table XIII refer to the numbered localities given in Table XII, which was drawn up to avoid a cumbersome repetition in Table XIII of geographical localities.

The value of the palæobotanical evidence for our present purpose depends largely upon the soundness of the identifications. This point will, therefore, be reviewed before we proceed to draw any conclusions from the fossil record.

The first part of Table XIII is occupied mainly by the records of the Reids. In all these cases the fossils were fruits which, after being preserved by special methods, were examined for the details of structure, such as shape, ribs, sculpture, etc. It may appear strange that determination of such fossils can be made with specific accuracy, especially in large genera such as

Eupatorium and *Senecio*. The method apparently followed by these authors of comparing the fossil fruits in the first instance with the fruits of species now existing in the same localities avoids the difficulties and uncertainties which would undoubtedly arise if the comparison were wider. It is seldom impossible but sometimes very difficult to assign recent well-preserved fruits to a particular species. The deposits dealt with are, however, comparatively recent, and the limited comparison is, therefore, probably quite justified and the determinations can be accepted as accurate.

Opinions differ on the exact age of the peperino from which the leaves of *Tussilago Farfara* are described by Antonelli (cp. 15). As that tufa is, however, certainly post-glacial and the fruits are recorded from both neolithic and Cromerian beds the determination of these very distinctive leaves can be taken as corroborated by Reid's evidence. Antonelli's record of *Bellis perennis* from the same locality, although not corroborated in the same way, may be accepted.

The second part of Table XIII is occupied by a series of unclassified genera and species which require more critical consideration. The genus *Baccharites* of Saporta rests on a resemblance of these fossil leaves to those of *Baccharis*. For present purposes they may be classed with the *Silphium*-like leaves described by Massalongo as *Silphidium*. Bentham's comment (see Table XIII) on the identification of these leaves is echoed by more than one palæobotanist. The fossil leaves of *Hieracites Salyorum*, Sap. and *Parthenites priscus*, Sap. appear to the writer to be very probable determinations resting on much the same ground as Reid's identifications. The leaves of *Hyoserites Lingua*, Ettingsh, associated as they are with beaked achenes, seem to be the most authentic Compositæ leaves of the older strata.

The other fossils are chiefly fruits; *Bidentites antiquus* as figured by Heer (2, Pl. 101, Fig. 20) and Zittel (38, Fig. 404), is a fruit with a bidentate apex, but there its similarity to the fruits of *Bidens* ends. The teeth or awns arise close together on the contracted apex of the fruit and diverge at an angle rarely met with in *Bidens*, where the awns are erect, almost parallel and arise on opposite sides of a more or less truncate apex. The identification would certainly not survive the application of the criteria adopted by the Reids.

Carpolithus hyoseritiformis, Berry, is placed by its author among the genera "incertæ sedis" (3, p. 353), at the same time he says "it is almost certainly an achene of some Wilcox species of Compositæ." As figured and described by Berry this fruit has the characteristic

ridges and is crowned by about ten bristles which have lateral projections like those of *Coreopsis*. This solitary American representative would seem, therefore, to belong to the Helianthæ, if it is a Composite at all.

The large genus *Cypselites*, Heer, includes some undoubted Compositæ. Saporta's determinations may be accepted as being accurate in most cases, but those by Heer require critical revision. Saporta left the position of the gypsum beds to be decided by later workers. Zeiller (37) gives the period as lower Oligocene, while Ward (36) gives it as Eocene. *C. bisulcatus*, because of the paucity of the ridges, and *C. ellipticus*, because of the numerous ridges, although possibly Cynareæ, come under suspicion, which is increased by the curious projections from the beak in both cases. *C. Lessingii* also has very numerous ridges and a very peculiar group of rigid hairs. *C. rostratus* might also be excluded from the present discussion because of the absence of the characteristic ridges and the peculiar irregularity in length of the hairs. Some of these exclusions may seem severe but only thoroughly authentic Compositæ can be admitted for the purpose of elucidating the past history of the family. The genera *Hieracites* and *Hyoserites* contain several interesting species, all of which may be accepted as well defined Compositæ.

One of the most striking features of the well authenticated fossil Compositæ is the predominance of the simple setose type of pappus. Although the American Tertiary has as yet yielded practically no Compositæ, and the European forms, even from the Lower Oligocene, cannot be accepted as the earliest types, the evidence, as far as it goes, supports the view that the setose type of pappus is the primitive form (cp. Chap. V). The plumose setæ of *Cypselites Regelii* and *C. Ungerii*, the outer setæ with flattened, dilated bases (paleaceo-setose) of *Hyoserites Schultzii*, of *C. gypsorum* and those of *C. costatus* which are connate at the base, are all comparatively primitive types according to the view expressed in Chapter V.

In connection with the writer's opinion that the small, almost flat receptacle is the primitive type (see Fig. 19 and Chap. VI, B), it is noteworthy that the earliest known receptacula (*Hieracites stellatus* and *H. nudatus*) are small and almost flat. Concerning the latter species, which is interpreted as a receptacle with only the scar of the involucre showing and no bracts, but a densely packed mass of florets or achenes, Saporta (32b, p. 57) says "L'empreinte est difficile à interpréter." The figure (Pl. 20, Fig. 5a) which he gives, however, is quite clearly a typical Cichoriaceous cap-

itulum just before anthesis. The calyculus in that group is frequently soft, herbaceous and easily removed without disturbing the rest of the capitulum. The narrow, elongated structures on the outside of the fossil are too flat and undulate to be achenes: on the other hand they cannot be florets because they are attached directly to the receptacle without the least vestige of an ovary. The writer suggests, therefore, that this fossil is a capitulum with only the outer bracts or calyculus missing, and that it shows a sub-biseriate involucre similar to that which is the chief part of the fossil *Hieracites stellatus*, but with the equal involucral bracts which are common in the Cichoriæ.

We have, then, two fossil examples of involucre, *H. stellatus* and *H. nudatus*, which are both sub-biseriate. The latter is of a Cichoriaceous type but the former, although compared by Saporta with that of *Inula pulicaria*, is very closely similar to the involucre of *Senecio glaucus* figured above (Chap. VII, Fig. 21). Leaving the exact affinity as impossible to determine in the meantime, one point is clearly proved, namely, that the only involucre known in the fossil condition are sub-biseriate, and one of them shows the scar of a distinct calyculus. This is in accordance with the view expressed in Chap. VI, B, on the primitiveness of the involucre with an uniseriate pericline and a slightly developed calyculus.

Considering now the evidence which has a bearing on the dates of appearance in Europe of the various tribes, we find the Cichoriæ indicated by a number of beaked achenes, by the capitulum of *Hieracites nudatus*, and by leaves similar to those of recent species of the tribe. These occur in the lower Oligocene, so that, if the views expressed in Chap. X on the successive origin of the tribes from the Senecioneæ are correct, most if not all of the tribes had been differentiated at the beginning of the Oligocene period. The absence of any fossils from the Aix deposits which could be ascribed to the Calenduleæ or Arctotideæ, although only negative evidence, is interesting on account of the suggestion in Chap. X, D, of the origin of these tribes at a later date than that of the Cichoriæ. The decided development of the Cichoriæ in Oligocene and Miocene times is in accordance with the occurrence of a number of the same tribe in the Pliocene and later floras. An interesting point in connection with the suggested age of the genus *Lactuca* (Chap. X, C, and Fig. 31) is the similarity of *Cypselites spoliatus* to the fruits of that genus. The Asiatic affinity of two species of *Crepis* from the Middle Pliocene is in accordance with the suggested migration of the present Asiatic Cichoriæ from the Mediterranean region. The absence of any fossil species of

Hieracium, except *H. Pilosella*, is in accordance with the suggested recent origin by mutation of the thousands of micro-species described in that genus.

Although no palæobotanist has yet suggested an affinity between any of the earlier fossil Compositæ and Senecioneæ, it is significant that an unidentified species of *Senecio* is described by the Reids from the lowest beds (Middle Pliocene) examined by them. Quite a number of the fruits figured by Heer and Saporta might well be ascribed to *Senecio* and its allies.

The presence of the Cynareæ in the Mediterranean region in Miocene times and the absence of any clear evidence of their development in the Oligocene is in accordance with the date of origin as deduced from the structure and geographical distribution of the tribe. They are more restricted in area and more specialised in structure than the Cichorieæ, so that the action of the Law of Age and Area, as shown by the present distribution, receives some corroboration in this case from the fossil evidence. It will be noticed that both *Centaurea* and *Carduus* occur in the Upper Pliocene, so that the development of the Cynareæ at that date is in accordance with the greater age of the two sub-tribes represented.

The leaves of *Parthenites priscus* are so much like the characteristic leaves of species of *Chrysanthemum* that they may be used as corroborative evidence for the statement in Chap. X, D, that the main genera of the Chrysanthemidinæ are older than those of the Anthemidinæ, while the suggestion that the tribe arose before the Cichorieæ is not invalidated by the simultaneous occurrence of representatives of both tribes in the Lower Oligocene. The coroniform pappus of *Hyoserites Schultzei* from the Upper Miocene may be another indication of the presence of the Anthemideæ in these early times, while the occurrence of living species of the tribe in the early glacial deposits is further evidence of an antecedent development of the group.

The Inuleæ are represented only by an unidentified species of *Helichrysum* from the Middle Pliocene. Such meagre evidence is of little phyletic value; that the fruit belongs to the Gnaphaliinæ is in accordance with the views previously expressed on the primitiveness of that sub-tribe, while the absence of other representatives of the group, especially of *Gnaphalium*, is easily accounted for by the small size of the fruits and the alpine habitat of most species.

The Astereæ are represented only by the leaves of one living species and the fruits of another. As they are both Pleistocene they give no interesting data. The well confirmed derivation of the Eupatorieæ from the Astereæ, however, lends a double

interest to the records of *Eupatorium*. *E. cannabinum*, which occurs all over the Eur-Asiatic region at the present time, seems to have been common in England in Pleistocene times, another small piece of evidence supporting the Law of Age and Area. The obscure variety of *E. japonicum* is interesting, but, as the identity is not fully verified, no special conclusion can be drawn, since it is quite possible that the fossil fruit represents an old derivative of *E. cannabinum*, rather than the former extension of the living, local variety of *E. japonicum*. The Middle Pliocene development of *Eupatorium*, when considered in relation to the ancestry of the tribe, can, however, be taken as evidence in favour of the relatively early origin of the Asterææ.

The Helianthææ are represented by *Bidens* from the Upper Pliocene to the Roman Period. The wide extension of this genus at such a date, combined with the Lower Eocene Helianthoid *Carpolithus hyoseritiformis*, indicates an early origin of the Helianthææ as suggested in Chap. X, D. The available evidence concerning the development of the Compositæ in America is, however, so meagre that it does not furnish any information about the relative age in America of the various tribes. This field for research is still very open and investigations on the early Tertiary Compositæ of America would prove very interesting.

From the above brief account of fossil Compositæ it will be seen that so far as our present knowledge extends the details are quite in accordance with the phyletic suggestions given in previous chapters; they add little, it is true, but slight confirmation is all that can be expected from such an incomplete record.

According to Chamberlin and Salisbury (6) the Angiosperms arose in late Jurassic or early Comanchean times in the eastern part of North America. This theory is regarded by Stopes (34) as possibly true but unproven (35). The evidence of the present geographical distribution of most of the Sympetalæ and of the higher Archichlamydeæ is in favour of a more southern place of origin—the northern part of South America. Fossil evidence is scanty, but other data point quite clearly to the region of the Amazons and northern Andes as the geographical source of the Angiosperms in general and of the Compositæ in particular.

Late Cretaceous or early Eocene times are indicated as the time of origin of the Compositæ. This is in agreement with the suggested early Tertiary origin deduced by Guppy (IX, 21, p. 245) from the absence of endemic genera of Compositæ from the Fiji Islands and their presence in the Hawaiian Islands. That phenomenon, however, can be explained equally well by the

hypothesis of an immigration of Compositæ into the Fiji Islands from the east at a date much later than the migration from America of the ancestors of the Hawaiian endemics. The peculiar, insular endemic genera occur on the islands (Galapagos, Juan Fernandez and Hawaiian) which are much nearer America than Fiji. The last mentioned probably received its present Compositæ after New Zealand had been stocked from New Guinea via Australia (see Chap. X).

It has been shown above that the migration of most of the Compositæ, and of *Senecio* in particular, took place along the mountain ranges. The dispersal of the Compositæ must, therefore, have taken place after the formation of the ridges which constitute the main path of migration. According to the geological evidence

TABLE XII.

List of Localities for the Records in Table XIII.

Pleistocene	Roman Period Neolithic	1. Silchester, Hampshire 2. Redhall, near Edinburgh 3. Hailes, " " 4. Fillyside " " 5. Gayfield " " 6. Close y Garey, Isle of Man 7. Elie, Fife 8. Tilbury Docks, Essex
	Paleolithic Post-Glacial Late Glacial	9. Reuver, (alluvial beds) see 31 10. Albano, Rome 11. Angel Road, Lea Valley 12. Hedge Lane, " 13. Ponder's End " " 14. Temple Lane, " 15. Hoxne (bed C), Suffolk 16. Hailes (lower bed), near Edinburgh 17. Corstorphine, near Edinburgh 18. Garvel Park, Clyde Beds 19. Roxburgh Street, Greenock
	Interglacial	20. Allenton, near Derby 21. West Wittering, Sussex 22. Southelmham, Suffolk 23. Hoxne (bed D), Suffolk 24. Shacklewell, London 25. Hitchin, Hertfordshire 26. Beeston, Norfolk
Upper Pliocene	Early Glacial (Arctic Plant Bed) Cromerian Beds	27. Pakefield, Suffolk 28. Mundesley, Norfolk 29. Tegelen, Limburg
Middle Pliocene	Teglian Beds Reuverian Beds	30. Swalmen, Dutch-Prussian Border 31. Reuver, " "
Upper Miocene	—	32. Oeningen, near Constance " " 33. Rochesauve, Ardèche 34. Priesen, Bohemia 35. Savine (Stellen), Alps
Middle Oligocene	—	36. Chiavon, Vicentin, Italian-Tirol frontier 37. Salcedo " " "
Lower Oligocene	—	38. Aix en Provence 39. Gergovie, Puy-de-Dôme
Lower Eocene	Wilcox Beds	40. Puryear, Henry County, Tenn.

TABLE XIII.

List of fossil fruits, leaves, etc., which have been classed as Compositæ.

Species Classified.	References.	Dates and Localities.	Remarks.
SENECIONEÆ TUSSILAGININÆ <i>Tussilago farfara</i> , L.	Reid, 22, 23 Antonelli, 1 Zittel, 38 Reid, 27	Neolithic, 2 Post Glacial, 10 Upper Pliocene, 27	Only one fruit Leaves in volcanic tufa [or peperino] Fruits
SENECIONINÆ <i>Senecio aquaticus</i> , Huds. „ <i>syriaticus</i> , L. <i>Senecio</i> sp. CICHORIEÆ LAPSANINÆ <i>Lapsana communis</i> , L.	Reid, 23 Reid, 22, 23 Reid, 29 Bentham, 2 Reid, 22, 23 „ 17, 22, 23 „ 16, 22, 23	Interglacial, 21 Neolithic, 2 Middle Pliocene, 30 Upper Miocene Neolithic, 2, 3 Interglacial, 21 Upper Pliocene, 27	Near <i>S. sylvaticus</i> Heer's species of [Cypselites]
CREPIDINÆ <i>Picris hieracioides</i> , L. <i>Crepis</i> cf. <i>blattaroides</i> , Vill.	Reid, 16, 22, 23, 27, 29 Reid, 29	Upper Pliocene, 27 Middle Pliocene, 30	Very near <i>C. blattaroides</i> but also resembles cer- tain spp. of China
<i>Crepis fuscipappus</i> , Benth. <i>Crepis succisefolius</i> Tausch. <i>Crepis virens</i> , L.	Reid, 29 Reid 27, 29 Reid 22, 23 „ 30 „ 29 „ 25	Middle Pliocene, 30 Upper Pliocene, 27 Neolithic, 2 Late Glacial, 11 Middle Pliocene, 31 Paleolithic, 9	A mountain species of India & Chinese forests Not uncommon In alluvium
HIERACINÆ <i>Hieracium pilosella</i> , L.	„ 23	Interglacial, 21	No trace of any other species of <i>Hieracium</i> has been found fossil in [Britain]
HYPOCHÆRIDINÆ <i>Leontodon autumnalis</i> , L. <i>Leontodon hispidus</i> , L. <i>Taraxacum officinale</i> , Web.	Reid 22, 23 „ 30 „ 22, 23 „ 27, 29 „ 24a „ 22, 23 „ 19, 22, 23 „ 22, 23 „ 22, 23 „ 22, 23 „ 22, 23 „ 30	Neolithic, 2 Late Glacial, 12, 13 Interglacial, 20 Upper Pliocene, 27 Roman Period, 1 Neolithic, 2, 4 Late Glacial, 15 „ „ 16, 17, 18 „ „ 19 Interglacial, 20, 21, 22 Late Glacial, 11, 12, 13, 14	Rare 4 is a raised beach In glacial clay
LACTUCINÆ <i>Sonchus arvensis</i> , L. <i>Sonchus oleraceus</i> , L. „ <i>palustris</i> , L.	„ 18, 22, 23 „ 22, 23 „ 24a „ 24a	Neolithic, 2, 5 „ Roman Period, 1 „ „ 1	Lacustrine deposits of Scottish lowlands
ANTHEMIDEÆ CHRYSANTHEMIDINÆ <i>Chrysanthemum</i> <i>Leucanthemum</i> , L. <i>Chrysanthemum segetum</i> , L. <i>Matricaria inodora</i> , L.	Reid 23, 24a „ 18, 22, 23 „ 18, 22, 23	Roman Period, 1 Neolithic, 2, 3 Neolithic, 2, 3	

TABLE XIII (continued)

Species Classified.	References.	Dates and Localities.	Remarks.
<i>Tanacetum vulgare</i> , L.	Reid, 22, 23	Early Glacial, 26	Base of Arctic Fresh- [water beds]
INULEÆ			
GNAPHALINÆ			
<i>Helichrysum</i> , sp.	Reid, 29	Middle Pliocene, 30	Similar to several species
CYNAREÆ	Bentham, 2	Upper Miocene, 32	Two or three of Heer's species of <i>Cypselites</i>
CARDUINÆ			
<i>Arctium Lappa</i> , L.	Reid, 24a	Roman Period, 1	
" sp.	" 27	Upper Pliocene, 27	Two different forms
<i>Carduus crispus</i> , L.	" 22, 23	Neolithic, 6	Bed B
" <i>nutans</i> , L.	" 24a	Roman Period, 1	
	" 30	Late Glacial, 13	
	" 27, 29	Upper Pliocene, 27	Not uncommon
	Zittel, 38		
" cf. <i>nutans</i> , L.	Reid, 27, 29	Upper Pliocene, 27	Differs in sculpture and absence of long- itudinal ridges.
	" 26	Upper Pliocene, 29	
" sp.	" 29	Middle Pliocene, 31	Near <i>C. nutans</i>
" sp.	" 25	Paleolithic, 9	In alluvium
<i>Cnicus lanceolatus</i> , Willd.	" 24a	Roman Period, 1	
	" 24b	" "	In two places, in a well and in a pot
	" 22, 23	Neolithic, 2	Fruits rather small
	" 22, 23	" 7	
	" 17, 22, 23	Interglacial, 21	
	" 16, 27	Upper Pliocene, 27	Recorded in 16 with a ? as rare, fruit small
<i>Cnicus (Carduus) sp.</i>	" 29	Middle Pliocene, 31	Near <i>C. lanceolatus</i>
" <i>palustris</i> , Willd.	" 23	Neolithic, 3	
	" 22, 23	" 2	
	" 30	Late Glacial, 11	
	" 22, 23	Interglacial, 22	Fruits small
	" 27	Upper Pliocene, 27	
	" 28	" 29	
<i>Cirsium heterophyllum</i> , Hill.	" 27, 29	" " 27	
CENTAUREINÆ			
<i>Centaurea Calcitrapa</i> , L.?	" 27, 29	" " 27	One of two forms found
" <i>Cyanus</i> , L.	" 18, 22, 23	Neolithic, 2	
" sp.	" 27	Upper Pliocene, 27	The other of two forms found
ASTEREÆ			
BELLIDINÆ			
<i>Bellis perennis</i> , L.	Antonelli, 1 Zittel, 38	Post Glacial, 10	Leaves in volcanic tufa [or peperino]
HETEROCHROMINÆ			
<i>Aster Tripolium</i> , L.	Reid, 23	Interglacial, 21	
EUPATORIÆ			
AGERATINÆ			
<i>Eupatorium cannabinum</i> , L.	" 22, 23	Neolithic, 8	In peat below sea-level
	" 22, 23	" 2	
	" 19, 22, 23	Late Glacial, 15	Bed C in "blackearth," below Paleolithic de- posits
	" 17, 23	Interglacial, 21	
	" 21, 23	" 24	In peaty clay below 8 or 10 ft. of gravel
	" 20, 23	" 25	Ancient alluvium, below Paleolithic brickearth

TABLE XIII (continued)

Species.	References.	Dates and Localities.	Remarks.
<i>Eupatorium cannabinum</i> , L.	Reid, 19, 22, 23	Interglacial, 23	Bed D, in lignite, below bed C
<i>Eupatorium japonicum</i> , Thunb. var.	" 23 " 29	" 20 Middle Pliocene, 30, 31	Very near to, if not identical with a variety collected in the mountains of Japan
<i>Eupatorium</i> , sp. HELIANTHÆ COREOPSIDINÆ <i>Bidens cernua</i> , L. " <i>tripartita</i> , L.	" 27, 29 " 22, 23 " 24a " 19, 22, 23 " 19, 22, 23	Upper Pliocene, 27 Neolithic, 2 Roman Period, 1 Late Glacial, 15 Interglacial, 23	Bed C, a starved fruit Bed D, associated with a variety with four equal awns
"	" 16, 23 " 27, 29	Upper Pliocene, 28	
"	" 16, 23, 27 Zittel, 38	" " 27	
<i>Bidens tripartita</i> , L. var. UNCLASSIFIED Genus ?	Reid, 23, 28 " 19	" " 29 Interglacial, 23	Bed D, four equal awns
Genus ?	Reid, 29	Middle Pliocene, 31	Fruit poorly preserved and apparently germinated
"	" 29	" " 30	Fruit of some large Composite, but apex not preserved and base obscure
<i>Baccharites</i> , Sap. = <i>Lomatites</i> , Sap. (part.)	Saporta, 32b Zeiller, 37 Zittel, 38	Lower Oligocene, 38	Leaves like those of <i>Baccharis</i> and other Conyzinæ, first referred to Proteaceæ
<i>B. acerosus</i> , Sap.	Saporta, 31b, 31k, 32b Ward, 36 Zittel, 38	" " 38	
<i>B. aquensis</i> , Sap.	Saporta, 31b, f, k, 32b Ward, 36 Zittel, 38	" " 38	
"	Boulay, 5	" " 39	
<i>B. obtusatus</i> , Sap.	Saporta, 31k, 32b Ward, 36 Zittel, 38	" " 38	
<i>B. salicinus</i> , Sap.	as above	" " 38	
<i>B. sinuatus</i> , Sap.	Saporta, 31b, k, 32b Ward, 36 Zittel, 38	" " 38	
<i>Bidentites</i> , Heer.	Heer, 11 Bentham, 2	Upper Miocene, 32 " "	Heer's specimens, "probably the achene of an aquatic species"
<i>B. antiquus</i> , Heer.	Zeiller, 37 Heer, 11 Schimper, 33 Zittel, 38	Upper Pliocene Upper Miocene, 32	Reid's achenes of <i>Bidens</i>

TABLE XIII (continued)

Species.	References.	Dates and Localities.	Remarks.
<i>Carpolithus hyoseritifformis</i> Berry	Berry, 3	Lower Eocene, 40	Fruit 8 mm. long, with about 10 simple awns or bristles; among "Incertæ Sedis."
<i>Cypselites</i> , Heer.	Heer, 11 Saporta, 31, 32 Zeiller, 37	Upper Miocene, 32 Lower Oligocene, 38	Fruits of Compositæ
<i>C. angustatus</i> , Herr.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 8 mm. long, pappus 16 mm., sparse and setose, resembling <i>Crepis</i> fruits. Ettingshausen says this is like fruit of <i>Echitonium</i> .
<i>C. aquensis</i> , Sap.	Saporta, 32b	Lower Oligocene, 38	Achene 6.5 mm. long, pappus of scabrid setæ, longer than achene, very rare.
<i>C. bisulcatus</i> , Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 6mm. long, pappus stipitate, duplex, of slightly wavy setæ, 13 mm. long
<i>C. brachypus</i> , Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 8mm. long, pappus stipitate, beak short, setose, 19 mm. long.
<i>C. cincinnatus</i> , Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 8mm. long, pappus 20 mm. long, of numerous wavy setæ, connate at the base.
<i>C. costatus</i> , Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 9mm. long, pappus 18mm. long, of setæ connate at the base. Greatly resembles <i>Arctium lanuginosum</i> of central Europe (Heer, 9)
<i>C. deletus</i> , Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Pappus twice length of the achene. Probably <i>Cynareæ</i> (Heer, 9)
<i>C. dubius</i> (Al. Br.) Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	= <i>Achenites dubius</i> , Al. Br., achene 7mm. long, pappus slightly longer.
<i>C. ellipticus</i> , Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 7mm. long, pappus shortly stipitate, of very long slightly curved setæ. Compared with <i>Sonchus</i> by Heer, 9.
<i>C. elongatus</i> , Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 17 mm. long, shortly beaked.
<i>C. Fischeri</i> , Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 6mm. long, pappus 18 mm. long, of slightly wavy setæ. Perhaps a species of <i>Arctium</i> , Heer, 9
<i>C. fractus</i> , Sap.	Saporta, 32b	Lower Oligocene, 38	Pappus of very fine setæ, shorter than the achene, very rare.
<i>C. grandis</i> , Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 11 mm. & pappus 21mm, long, shortly stipitate, setose.
<i>C. gypsorum</i> , Sap.	Saporta, 31 b, k Schimper, 33 Ward, 36 Zittel, 38	Lower Oligocene, 38	Achene small & ribbed, pappus duplex, inner setæ numerous, outer 5-7 with dilated bases,

TABLE XIII (continued)

Species.	References	Dates and Localities	Remarks.
<i>C. latinus</i> , Massal.	Meschinelli, 14	Middle Oligocene, 37	Name only, quoted from Massalongo, Syll. pl. foss. p. 126
<i>C. Lessingii</i> , Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 7 mm. long, pappus stipitate, of thick, rigid setæ
<i>C. Miegi</i> , Fliche	Fliche, 8a	(Tertiary)	In chalk or hard marl at Riedisheim, Mulhouse. Like <i>C. Ungeri</i>
<i>C. Nageli</i> , Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Pappus twice as long as achene, obliquely inserted (cp. I, 7), of wavy setæ. Probably <i>Cynareæ</i> , Heer 9
<i>C. Philiberti</i> , Sap.	Saporta, 31k	Lower Oligocene, 38	Achene 5 mm. long, pappus setose
<i>C. Regelni</i> , Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 15 mm. long, pappus 15 mm. long, of plumose setæ, obliquely inserted (cp. I, 7)
<i>C. rostratus</i> , Heer.	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 8mm. long, pappus stipitate, setose
<i>C. Schultzii</i> , Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Achene 7 mm. long, pappus 18 mm. long, of numerous curved setæ
<i>C. spoliatus</i> , Sap.	Saporta, 32b	Lower Oligocene, 38	Achene 6 mm. long, no trace of pappus but a very obtuse beak, very rare. Rather like <i>Lactuca</i> with pappus off, Saporta, 32b
<i>C. stenocarpus</i> , Sap.	Saporta, 31k	Lower Oligocene, 38	Whole fruit 1.5 cm. long, pappus sessile, of compact setæ, very rare
<i>C. striatus</i> , Heer	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 8 mm. long, pappus 21 mm. long, stipitate, setose
<i>C. tenuirostratus</i> , Sap.	Saporta, 32b	Lower Oligocene, 38	Achene 5 mm. long, with truncate beak and no pappus, very rare
<i>C. tenuis</i> , Heer.	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 4.5 mm. long, pappus shorter, of wavy setæ
<i>C. trisulcatus</i> , Sap.	Saporta, 32b	Lower Oligocene, 38	Achene 7 mm. long, pappus sessile, only vestiges left, very rare
<i>C. truncatus</i> , Heer	Heer, 11 Schimper, 33 Zittel, 38	Upper Miocene, 32	Pappus twice as long as fruit. Probably <i>Cynareæ</i> , Heer, 11
<i>C. Ungeri</i> , Heer	Heer, 11 Schimper, 33	Upper Miocene, 32	Achene 16mm. long, pappus markedly stipitate, of elongated plumose setæ, compared to <i>Podospermum laciniatum</i> , Heer, 2
<i>Cypselites</i> , sp.	Boulay, 4	Upper Miocene, 33	Not identified with any spec. described by Heer
<i>Hieracites</i> , Sap.	Saporta, 32b Zeiller, 37	Lower Oligocene, 38	Defined by Saporta (32b) as the receptacle and involucre of fossil <i>Compositæ</i> .

TABLE XIII (continued)

Species.	References	Dates and Localities	Remarks
<i>H. stellatus</i> , Sap.	Saporta, 32b Zittel, 38	Lower Oligocene, 38	Avignon, in calcareous marl, very rare. Sub-biseriate involucre and small receptacle, compared to <i>Inula Pulicaria</i> and referred tentatively to that genus by Saporta
<i>H. nudatus</i> , Sap.	Saporta, 32b Zittel, 38	Lower Oligocene, 38	Receptacle after flowering, with involucre bracts missing & achenes or florets densely packed, Saporta, cp. text
<i>H. Salyorum</i> , Sap.	Saporta, 31b Schimper, 33 Zittel, 38	Lower Oligocene, 38	Leaves in marly schist above gypsum beds; compared by Saporta with <i>Taraxacum obovatum</i> .
<i>Hyoserites</i> , Ettings.	Ettingshausen, 7 Schimper, 33	Upper Miocene	In plastic clay, achenes like those of the "Hyoseridées"
<i>H. Lingua</i> , Ettings.	Ettingshausen, 8	Upper Miocene, 35	Achenes lanceolate acuminate very shortly beaked, pappus absent, leaves also present
<i>H. Schultzii</i> , Ettings.	" 7 Schimper, 33 Zittel, 38	Upper Miocene, 34	Achenes, pappus short, coroniform and paleaceous
<i>Lychnophorites</i> , Martius	Bentham, 2		Since referred to a Monocotyledon of the <i>Vellozia</i> type
<i>Parthenites priscus</i> , Sap.	Saporta, 31b Schimper, 33 Ward, 36 Zittel, 38	Lower Oligocene, 38	Leaves compared by Saporta to <i>Chrysanthemum Parthenium</i> and <i>C. Hysterophorus</i>
<i>Silphidium</i> , Mass.	Massalongo, 13 Bentham, 2 Meschinelli, 14 Schimper, 33 Zeiller, 37 Zittel, 38	Middle Oligocene, 36	Leaves, like <i>Silphium laciniatum</i> (Massalongo); "it is probable that the four species are really only one" (Schimper); "a wild guess without a particle of evidence in support of it" (Bentham)
<i>S. gracile</i> , Mass.	Massalongo, 13 Meschinelli, 14 Schimper, 33	Middle Oligocene, 36	
<i>S. heteromallum</i> , Mass.	Massalongo, 13 Meschinelli, 14 Schimper, 33	Middle Oligocene, 36	
<i>S. Proserpinæ</i> , Mass.	Massalongo, 13 Meschinelli, 14 Schimper, 33	Middle Oligocene, 36	Also a variety, <i>subdenticulatum</i>
<i>S. Visianicum</i> , Mass.	Massalongo, 13 Meschinelli, 14 Schimper, 33	Middle Oligocene, 36	Compared to <i>Silphium gummiiferum</i> of N. America by Massalongo; also a variety, & <i>denticulatum</i>

the Andes had begun to appear in late Cretaceous times, the height being increased by the Miocene uplift all around the Pacific.

In the previous chapter it was shown that the origin of the Compositæ was most probably due to the ecological conditions

at high altitudes in the Andes. The palæobotanical evidence shows that the origin of the family took place at approximately the same date as the first upheaval of the Andes. This synchronising of events in climatic evolution with events in plant evolution is in accordance with Coulter's explanation of orthogenesis (see XI, 13, and Chap. XI, B). The rapidity of dispersal, which is characteristic of the family, would readily account for the appearance of representatives in the Mediterranean region within a geologically short interval of the origin of the earliest forms. The time available for this dispersal and the differentiation of the types is nearly the whole of the Eocene Period and opinions concerning even the approximate length of that period vary very considerably.

It is more than probable that the Compositæ were among the first arrivals in the new mountainous habitats (cp. Krakatau and Taal, Chap. X), and this would account, in part at least, for their predominance in those regions at the present time. The Compositæ, indeed, seem to have been formed with the mountains by the mountains for the mountains.

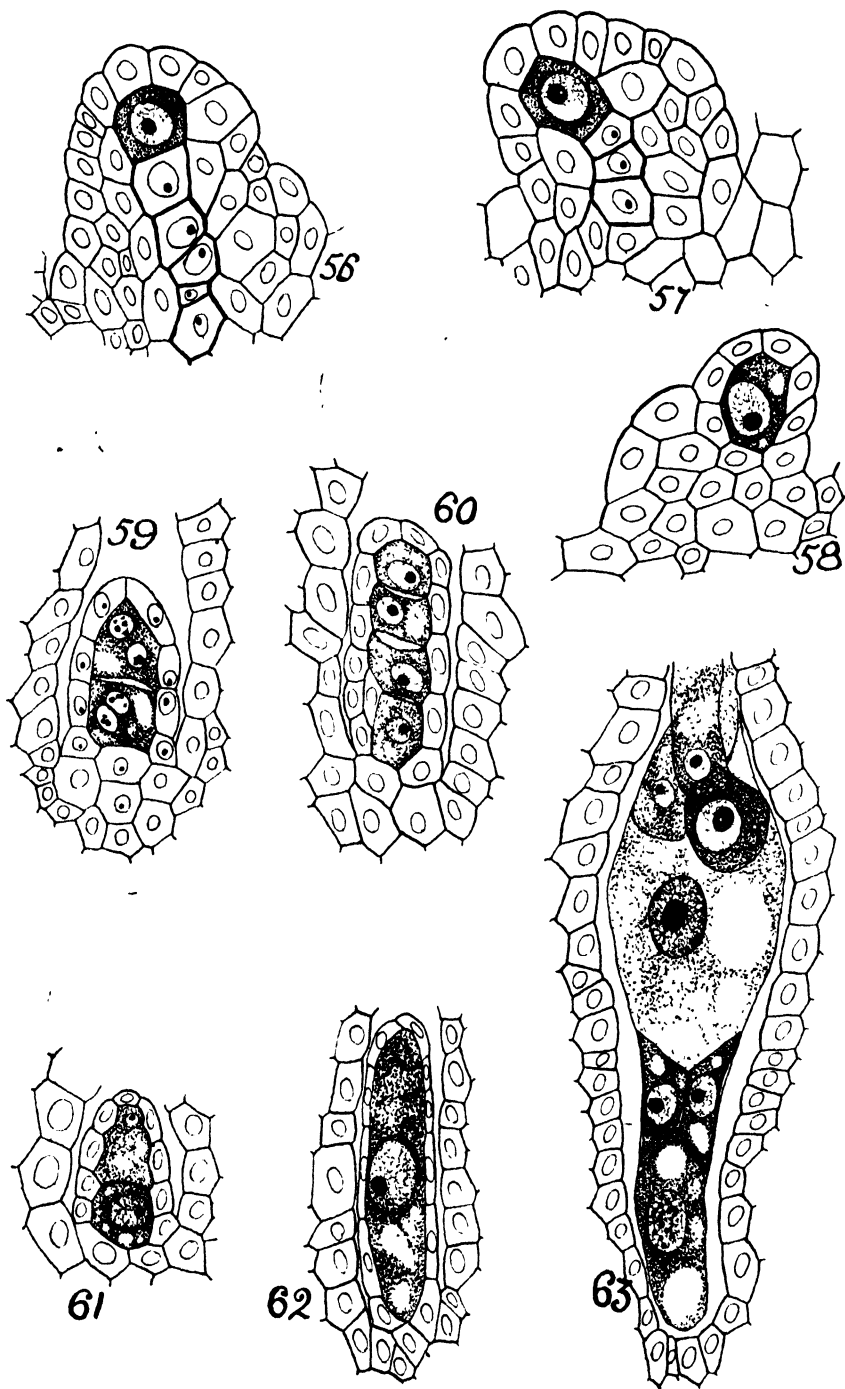
B. CYTOLOGY OF THE COMPOSITÆ.

This part of the subject has been worked out in considerable detail but only in a comparatively small number of genera. The chief papers will be found mentioned in Section B of Bibliography XII. Parthenogenesis, apogamy and double fertilisation have claimed attention but such data have little phyletic value, except as an explanation of the large numbers of microspecies in some of the genera. Spermatogenesis and oogenesis have been described in a number of forms and the figures given of *Senecio vulgaris* may be regarded as typical.

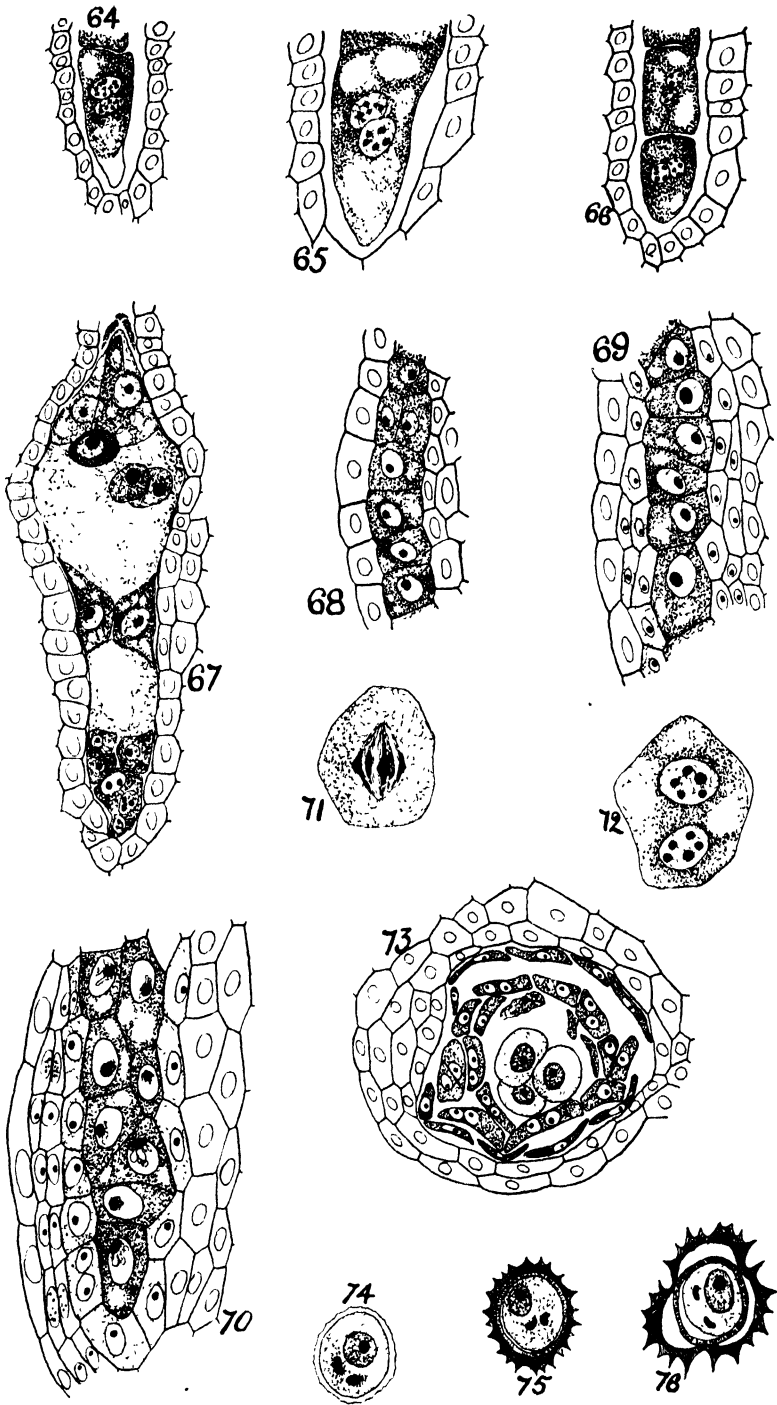
Spermatogenesis:—Considering spermatogenesis first, the archesporium is sub-epidermal, usually only one row of cells (Fig. 68), which cuts off a single layer outside (Fig 69). This layer divides into three (Figs. 69-70); the innermost of the layers forms the tapetum, the cells of which are frequently bi-nucleate (Figs. 70-73). The middle layer finally degenerates and functions as a subsidiary tapetum (Fig. 73). The single row of archesporial cells rarely undergo more than one division before the pollen mother cells are formed (Fig. 70), so that only one tetrad of microspores is usual in transverse sections of the sac (Fig. 73). The separation of the spore mother cells from each other takes place between synapsis (Fig. 70) and the metaphase of the reduction division (Fig. 71). The differentiation of the exine has already been mentioned (Chap. IV, B) as being sometimes intermediate in *Senecio* between the Tubulifloræ and the

Ligulifloræ (see Figs. 22-24). There is a large vegetative nucleus and two small, more or less vermiform male nuclei.

Oogenesis. Considering oogenesis next, the first controversial point is the cauline or lateral origin of the ovule. Most writers are



FIGS. 56-63. Oogenesis in *Senecio vulgaris*.

*Senecio vulgaris.*

FIGS. 64-67. Antipodal development. FIGS. 68-76. Spermatogenesis.

agreed that the single ovule belongs to one or other of the carpels, but Campbell (44) considers it to be primitively cauline. The cauline vascular bundle ends in a flattened or cup-shaped disc (cp.

11, 63), and the primitively lateral position of the ovule is confirmed by the anomalous cases figured by the writer (99) in which all the four lateral ancestral placentæ of the two carpels are indicated.

The single archesporial cell is differentiated at an early stage as the end cell of a row in the middle of the young ovule (Figs. 56-57). The integument shows an unilateral development almost from its first appearance (Figs. 56-58). While reduction division is taking place, the integument develops very rapidly, so that the following stages occur within a single-layered nucellus enclosed by the integument with its peculiar epithelium. A row of four megaspores is formed, with the middle or first formed wall very thick (Figs. 59-60). This wall disappears and the two middle megaspores degenerate (Fig. 61); the apical megaspore also degenerates and the basal one develops into the embryo sac (Fig. 62). Palm (84) considers that in *Solidago* and *Aster* the sac is formed from the micropylar megaspore and that the three lower megaspores develop into the haustorium. He is, however, adversely criticised by Chamberlain (49); and most other workers on the embryo sac of the Compositæ agree in describing the sequence of events as above.

This question has recently become rather controversial. Holmgren (64) describes six methods of embryo sac development in the Compositæ.

- A. with a row of four *cells* as megaspores,
 - (1). Sac from the chalazal megaspore, normal and eight-nucleate, as in most cases (69, 77, 91, 93, etc.);
 - (2). Sac from one of the other three megaspores and not always eight-nucleate, as in *Senecio vulgaris* (Winge, 113), *Solidago serotina* and *Aster novæ-angliæ* (Palm, 84), all three species with persistent megaspores in the antipodal region.
- B. With only one wall formed after the heterotypic nuclear division,
 - (3). Sac from the two micropylar megaspores, as in *Tanacetum vulgare* (Palm, 85);
- C. With no wall formed during meiosis;
 - (4). Sac from the micropylar megaspore nucleus and eight-nucleate, as in *Anthemis tinctoria* (Holmgren, 64);
 - (5). Sac from the two micropylar megaspore nuclei and eight-nucleate with persistent chalazal megaspores, as in *Tanacetum vulgare* (Palm, 85);

- (6). Sac from all four megaspore nuclei and sixteen-nucleate, as in *Pyrethrum parthenifolium* var. *aureum* (Palm, 85).

Winge's interpretation of his figures is rather unsatisfactory and has been shown to be wrong by Carano (47). In his English summary he states that three megaspores degenerate but in the text he figures and describes three large bi-nucleate megaspores and three very minute, degenerate antipodals in the region of the egg-apparatus. He considers that the micropylar megaspore develops into the embryo sac, but his Fig. 3 shows the chalazal megaspore slightly larger than the others, and his Fig. 4 shows three small megaspores and a large one, the row being isolated so that the micropylar or chalazal position of the large megaspore cannot be determined.

Winge's figures, apart from the very problematical degenerate antipodals, are similar to those given here and are best interpreted in a similar way, as Carano (46-47) and others maintain.

Palm's interpretation of the phenomena in *Aster* and *Solidago* has already been more or less discredited by Chamberlain (49). There remain the anomalies of types 3-6; these all occur in the Anthemideæ and it is possible that further investigations will confirm the presence in this tribe of anomalous embryo-sac development, as in *Plumbagella* (51), *Lilium*, etc.

The disappearance of the upper megaspores is very clear in *Senecio* and *Silphium*. Even in the interesting case of an aposporic embryo sac described by Rosenberg (90) in *Hieracium*, the tetrad was formed and the chalazal megaspore was the last to disappear before the nucellus was pushed on one side by the growth of the abnormal sac. The origin of the chalazal haustorium from the antipodals can be taken as without any properly authenticated exception.

In the mature embryo sac there is the normal arrangement of synergids, oosphere, endosperm or fusion nucleus, and three antipodals (Fig. 63). The nucellus disappears completely, leaving the embryo sac surrounded by the epithelial layer of the integuments, or a few remnants may be left to form the so-called nucellar cap (Fig. 67).

Antipodal Cells. In *Senecio vulgaris* the basal or chalazal antipodal elongates (Fig. 63) and divides (Figs. 64-67), the basal portion showing as many as four extra antipodal cells in one longitudinal section, each cell having one or more nuclei (Fig. 67). This is the structure of which it is said that "the antipodals of many of the Compositæ are organised into an aggressive haustorium

TABLE XIV

List of Antipodal Cells in Compositæ.

Species	Nos.	References	Remarks.
SENECIONEÆ TUSSLAGININÆ <i>Tussilago</i> sp.	4 usually	Guignard, 60 Coulter and Cham- berlain, 50 ditto	
<i>Petasites</i> sp.	3	ditto	Active and haustorial
SENECIONINÆ <i>Doronicum</i> sp.	3	ditto	"
<i>Cineraria maritima</i>	10-12	Goldflus, 58	Uniseriate, " polygonal or rounded, and contin- ued into pseudochalaza haustorial
<i>Senecio aureus</i>	3-6	Mottier, 78 C. and C., 50	
<i>S. Doria</i>	8-9	Goldflus, 58	Uniseriate, upper large lower pass gradually into chalazal cells
<i>S. vulgaris</i>	3	Strasburger, 101 Warming, 112	Normal arrangement, one chalazal & the other two side by side above Uniseriate
	3-4	Guignard, 61 Strasburger, 100	Normal or 4, uniseri- ate, the chalazal anti- podal having divided
	3-6	Small (Figs. 63-67)	Chalazal antipodal di- viding & multinucleate
<i>Cacalia hastata</i> (<i>Senecio</i>)	3	Goldflus, 58	Chalazal antipodal elongates to give tube
CICHORIEÆ HYOSERIDINÆ <i>Catananche lutea</i>	3	Goldflus, 58	Normal or uniseriate
<i>Cichorium Intybus</i>	3	Hegelmaier, 62	
HIERACIINÆ <i>Hieracium amplexicaule</i>	3	Hegelmaier, 62.	
HYPOCHOERIDINÆ <i>Hypochaeris maculata</i>	3	Hegelmaier, 62	
<i>Taraxacum officinale</i>	3	Schwere, 98	
	4-5	Hegelmaier, 62 C. and C., 50	Haustorial
<i>Taraxacum</i> sp.	3	C. and C., 50	Haustorial
LACTUCINÆ <i>Sonchus oleraceus</i>	3	Lavialle, I, 52	Uniseriate
SCORZONERINÆ <i>Tragopogon floccosus</i>	7-9	Hegelmaier, 62	Haustorial
<i>Scorzonera alpina</i>	3-4	Goldflus, 58	Haustorial, normal ar- rangement or with chal- azal antipodal divided
<i>S. hispanica</i>	4-7	Goldflus, 58	Haustorial
CALENDULEÆ <i>Calendula arvensis</i>	3	Carano, 46	One synergid develops into large micropylar haustorium
<i>C. lusitanica</i>	3	Billings, 42 C. and C., 50	ditto
ANTHEMIDEÆ CHRYSANTHEMIDINÆ <i>Pyrethrum balsaminatum</i> (<i>Chrysanthemum</i>)	3	Ward, 111	Normal
<i>Leucanthemum lacustre</i> (<i>Chrysanthemum</i>)	3-7	Goldflus, 58	In two rows, chalazal antipodal enlarges and shows abnormal nuclei as in <i>Senecio vulgaris</i>

TABLE XIV (continued)

Species.	Nos.	References.	Remarks
<i>Chrysanthemum Leucanthemum</i>	3	Goldflus, 58	Chalazal antipodal much enlarged and [elongated]
INULÆ GNAPHALINÆ <i>Antennaria alpina</i>	at least 19	Juel, 70 C and C. 50	Quite a tissue by continued division
INULINÆ <i>Inula Helenium</i>	6	Goldflus, 58	In two rows or scatter- [ed]
BUPHTHALMINÆ <i>Telekia speciosa</i> (<i>Bupthalmum</i>)	3	Goldflus, 58	All large, elongated chalazal gives a long [tube]
CYNAHEAE CENTAUREINAE <i>Serratula coronata</i>	3	Goldflus, 58	Uniseriate
<i>Centaurea cirrhata</i>	3	Lavialle, 1, 52	Uniseriate
<i>C. crocodylium</i>	3	Goldflus, 58	Normal
<i>C. dealbata</i>	4	Goldflus, 58	Uniseriate, haustorial
<i>C. macrocephala</i>	4	Goldflus, 58	Uniseriate, haustorial
ASTEREAE HOMOCHROMINAE <i>Solidago serotina</i>	3	Palm, 84	Haustorial, interpreted by Palm as the three chalazal megaspores
BELLIDINAE <i>Bellis perennis</i>	6-7	Carano, 45	One cell with 3 nuclei, another very large containing a pseudo-oosphere (cp. Chamberlain 48)
HETEROCHROMINAE <i>Aster Nova-Anglie</i>	3-13	Chamberlain, 48 C. and C., 50	Up to 20 nuclei in 1 cell pseudo-oosphere present [sphere]
<i>Galatella rigida</i> (<i>Aster</i>)	3-13	Goldflus, 58	No trace of pseudo-oo-
CONYZINAE <i>Conyza</i> sp.	20-25	Goldflus, 58	Forming a parenchyma
8-10	Guignard, 60 C. and C., 50	Haustorial	
HELIANTHEAE MELAMPODIINAE <i>Silphium</i> spp.	2-7	Merrell, 77	One case of 7 cells, 8 nuclei in one of them "with indications of amitotic divisions"
3-8	C. and C., 50		
ZINNINAE <i>Zinnia tenuiflora</i>	3-4	Hegelmaier, 62	Uniseriate or with upper cell divided
VERBESININAE <i>Dracopis amplexicaulis</i> (<i>Rudbeckia</i>)	3-4	Goldflus, 58	Uniseriate
<i>Echinacea intermedia</i> (<i>Rudbeckia</i>)		Goldflus, 58	A small number, polygonal
<i>Rudbeckia speciosa</i>	2-3	Nawaschin, 80	Two antipodals figured, one enlarged and very like an oosphere
<i>Helianthus annuus</i>	3	Hegelmaier, 62	Chalazal antipodal enlarged
2	Hofmeister, 63 Nawashin, 80 Carano, 46	Both cells large and elongated ditto ditto, upper cell multinucleate	
<i>H. Maximiliani</i>	3	Goldflus, 53	Uniseriate, upper antipodal enlarged & as long as the rest of the sac

TABLE XIV (continued)

Species	Nos.	References	Remarks
<i>H. tuberosus</i>	2 3	Goldflus, 58	Uniseriate
<i>Helianthus</i> sp.	3	Täckholm, 103	Chalazal antipodal degenerates but upper cell is very large and long
COREOPSIDINAE			
<i>Dahlia gracilis</i>	2-3	Goldflus, 58	Uniseriate or normal, binucleate or multinucleate
<i>Bidens leucantha</i>	3	Hegelmaier, 62	One small and two large
<i>Cosmos bipinnatus</i>	2	Täckholm, 103	Both large, 19 nuclei figured in one cell
<i>Cosmidium Burridgeanum</i> (Cosmos)	2	Täckholm, 103	Both large, one very long with 16-25 nuclei
HELENIEAE			
HELENIINAE			
<i>Gaillardia bicolor</i>	3	Goldflus, 58	Uniseriate, lower short, middle long and narrow, upper short

which can only be regarded as a very specialised organ" (50 p. 108).

In connection with the origin of the Compositæ from the Lobelioideæ it is interesting to note that an antipodal haustorium is recorded in *Campanula americana* (40), *C. rotundifolia* (39) and *Lobelia inflata* (97), and that most of the Campanulaceæ develop either micropylar or chalazal haustoria or both (50). Another point of similarity is that in both families the epithelium of the integument is conspicuous, always in the Compositæ, sometimes in the Campanulaceæ.

The general phylogenetic value of the endosperm and haustorium is considerable, as shown by Jacobsen-Stiasny (68). In the Compositæ the antipodal haustorium, presumably derived from the similar structure in the ancestral Lobelioideæ, has been described in a number of genera and the results, which are summarised in Table XIV, will now be discussed.

According to our present knowledge there are two methods by which the antipodals develop into a special haustorial apparatus, one by elongation and free nuclear division or amitosis or both, and the other by elongation accompanied by cell division giving a tissue. Both these methods occur to a certain extent in *Senecio vulgaris*.

The tube haustorium is more developed in other Senecioneæ (*Cacalia hastata*) and so is the tissue haustorium (*Senecio Doria* and *Cineraria maritima*). The Tussilagininæ have the haustorium only slightly developed.

In the Cichorieæ the haustorium is only slightly developed throughout, especially in the Lactucinæ; the exception is the advanced, rather special group, Scorzonerinæ.

In the Calenduleæ the antipodals are more or less normal but a special micropylar haustorium is developed.

The development of the haustorium in the Chrysanthemidinæ closely approximates to that in *Senecio*.

Although the data in the Inuleæ are very meagre, what there is tends to support the diphyletic development of that tribe, the Inulinæ being near the Senecioninæ and leading to the Centaureinæ through the Bupthalmiinæ.

In the Centaureinæ the slight development of the haustorium is rather surprising considering the advanced position of the tribe, but is, nevertheless, quite in keeping with the slight development of the haustorium in the ancestral Bupthalmiinæ.

The haustorium in the Astereæ is slightly developed in the primitive Homochrominæ, more developed in the more advanced Bellidinæ and Conyzinæ, and most developed in the advanced Heterochrominæ. An investigation of the antipodals of the Eupatorieæ should prove interesting in view of the derivation of that tribe from the Heterochrominæ.

The coenocytic tube type of haustorium is best developed in the Heliantheæ. The structure of the organ in the primitive Verbesininæ is sometimes quite simple and in most, if not all cases, it is less developed than it is in the Coreopsidinæ, especially *Cosmos*. The haustorium in the Zinniiinæ is simple, in the Melampodiinæ it is more developed (cp. Fig. 79).

The development, as far as it is known, in the Helenieæ agrees with the origin of that tribe from the Senecioneæ directly and not indirectly via the Heliantheæ.

In spite of the very restricted number of species in which the antipodal development is known, it is clear from the above that the data are drawn from sufficiently representative genera to furnish some interesting confirmation of previous phyletic suggestions.

Chromosomes. Meek's theory (76) of a constant diameter for the chromosome with a gradual elongation of each chromosome during evolution, and conjugation of the chromatin units, in fours when the length-limit has been reached, to give chromosomes with twice the original diameter, has been criticised by Farmer and Digby (54), who agree, however, that although the chromosome width cannot be strictly correlated with the evolutionary sequence, many of the lower animals and plants have smaller and narrower chromosomes, as compared with those of higher forms. The chromosome width varies so much in plants that it is certainly not very useful in dealing with phyletic within a family.

Apart however from these considerations, the variation in the

chromosome number in the Compositæ shows some interesting points. These numbers are recorded in various lists by Gates (57), Winge (114), and Ishikawa (66-67), and all the known numbers are given in Table XV. Tischler (109) and Winkler (115) have given general accounts of the phenomena, but they are not yet available. Winge (114) considers the Compositæ specially, distinguishing as cardinal numbers 9 for the Anthemideæ and 8 for the Heliantheæ; his classification of the genera seems, however, to be mainly on the chromosome number rather than on any generally accepted system, e.g., he puts *Bellis* in the Anthemideæ and *Calendula* in the Heliantheæ. Rosenberg (94) mentions the Compositæ series of numbers and shows how they may arise by unequal heterotypic divisions, with or without the formation of subsidiary nuclei with a small number of chromosomes.

The known chromosome numbers of the Compositæ are given in Table XV, with calculated numbers in brackets. Where no gametic number is given the species is apogamous and where a (v) is appended to the name of an author he has given verbal information to the authority quoted below.

Considering the numbers as given in Table XV, the first case is *Senecio vulgaris* for which Ishikawa (67) records 19. The present investigation shows 5 at reduction division, the metaphase (Fig. 71) is very clear and in the telophase (Figs. 59, 72) the number again appears as 5, with some indication of an idiochromosome which shows also in some of the divisions of the chalazal antipodal cell (Figs. 65-66). The anomalous nuclear divisions in the basal antipodal show other numbers also, about 20 (Fig. 63) or 10 (Fig. 64). As *S. vulgaris* is an aggregate species it is probable that Ishikawa examined some other member of the aggregate, in which apogamy or hybridisation may have led to complications. The figures 56-76 were drawn in 1914, when the writer was unaware of the only two examples of 5 then known as a chromosome number in the Compositæ, but quite a number of other examples with 5 have since been described.

It will be seen from Table XV that the 9, 18, 27, 36, 45 series holds good for all the Anthemideæ except *Achillea Millefolium*, in which the number is not known with certainty, and *Centipeda orbicularis*, which has 10. The series 8, 16, 32 likewise holds good for the Heliantheæ with certain exceptions.

If we seek any phyletic data in the chromosome numbers, the 5, 10, 15, 20, 30, 60 series is indicated as the primitive one in accordance with the phylesis of the family as shown by other data. This is the series of the Senecioneæ, with the cardinal number

TABLE XV.

Chromosome Numbers in the Compositæ.

Species.	Numbers		References
	Gametic	Somatic	
SENECIONEAE			
SENECIONINAE			
<i>Senecio vulgaris</i>	19		Ishikawa, 67
	5		Small, figs. 59, 65, 66, 71, 72
<i>S. sagittatus</i>	5		Ishikawa, 67
<i>S. nikensis</i>	10		"
<i>Ligularia tussilaginea</i>	30		Miyaji
(<i>Senecio</i>)			Ishikawa, 67
<i>L. tussilaginea</i> var. <i>crispata</i>	30, 31		Miyaji
			Ishikawa, 67
<i>L. japonica</i>	±60		Miyaji (v)
			Ishikawa, 67
CICHORIEAE			
LAPSANINAE			
<i>Lapsana humilis</i>	8		Ishikawa, 67
<i>L. apogonoides</i>	22		"
CREPIDINAE			
<i>Picris hieracioides</i>	5		"
<i>Crepis virens</i>	3	6	Rosenberg, 92
			Beer, 41
			Digby, 52
			Gates, 57
			Ishikawa, 66, 67
<i>C. tectorum</i>	4	8	Juel, 70
			Beer, 41
			Gates, 57
			Ishikawa, 67
<i>C. taraxacifolia</i>	4	8	Digby, 52
			Ishikawa, 67
<i>C. lanceolata</i> var. <i>platyphyl-</i>	5	10	Tahara and Ishikawa, 108
<i>C. japonica</i> [lum]	8	16	Tahara, 104
			Gates, 57
HIERACIINAE			
<i>Hieracium venosum</i>	7	14	Ishikawa, 66, 67
			Rosenberg, 91
			Gates, 57
			Ishikawa, 67
<i>H. auricula</i>	9	18	Rosenberg, 91, 94
			Gates, 57
			Ishikawa, 66, 67
<i>H. umbellatum</i>	9	18	Juel, 70
			Gates, 57
			Ishikawa, 66, 67
" (apogamous race)		27	Rosenberg, 94
<i>H. excellens</i>	17	34	Rosenberg, 91
			Gates, 57
			Ishikawa, 66, 67
	18+18+6	42	Rosenberg, 94
<i>H. Pilosella</i>	18	36	" "
<i>H. aurantiacum</i>	c. 18	c. 36	" "
<i>H. flagellare</i>	21	c. 42	" 91
			Gates, 57
			Ishikawa, 66, 67
<i>H. boreale</i>	27		Rosenberg, 94
<i>H. laevigatum</i>	27		" "
<i>H. lacerum</i>	27		" "
<i>H. pseudoillyricum</i>	27		" "
HYPOCHOERIDINAE			
<i>Taraxacum confertum</i>	8	16	Rosenberg, 93
			Gates, 57
			Ishikawa, 66, 67

TABLE XV (continued)

Species	Numbers		References
	Gametic	Somatic	
<i>T. platycarpum</i>	8	16	Osawa, 82 Ishikawa, 67
<i>T. officinale</i>	12-13	24-26	Juel, 70
	12-13	26-30	Gates, 57
	12-13	20-30	Ishikawa, 66, 67
<i>T. albidum</i>		36-40	Osawa, 82 Ishikawa, 67
LACTUCINAE			
<i>Lactuca denticulata</i>	5		Ishikawa, 67
<i>L. Keiskeana</i>	5		Miyaji Ishikawa, 67
<i>L. lanceolata</i>	5		"
" <i>var. platyphylla</i>	5		Tahara and Ishikawa, 108 Ishikawa, 67
<i>L. tamagawensis</i>	8, often 7		" "
<i>L. stolonifera</i>	8		" "
<i>L. villosa</i>	9		" "
<i>L. laciniata</i>	9		" "
<i>L. Thunbergia</i>	12, often 11		" "
<i>L. debilis</i>	24		" "
<i>Sonchus oleraceus</i>	16		" "
SCORZONERINAE			
<i>Tragopogon pratensis</i>	6		Beer, 41
	7		Ishikawa, 67
CALENDULEAE			
<i>Calendula officinalis</i>	14	28	Lundegardh, 74 Ishikawa, 66, 67 Winge, 114
<i>Calendula</i> sp.	16	32	Rosenberg, 88 Ishikawa, 66, 67 Winge, 114
ANTHEMIDEAE			
ANTHEMIDINAE			
<i>Achillea Millefolium</i>	24 ?	48 ?	Lundegardh, 74 Ishikawa, 66, 67 Winge, 114
<i>Anthemis tinctoria</i>	9	18	Lundegardh, 74 Holmgren, 64 Ishikawa, 66, 67 Winge, 114
CHRYSANTHEMIDINAE			
<i>Chrysanthemum carinatum</i>	9		Tahara, 106 Ishikawa, 74 Winge, 114
<i>C. coronarium</i>	9		ditto
<i>C. japonicum</i>	9		ditto
<i>C. lavandulæfolium</i>	9		ditto
<i>C. lineare</i>	9		Tahara (v) Ishikawa, 67
<i>C. Marchalli</i>	9,		Tahara, 106 Winge, 114
<i>C. myconis</i>	9		Tahara (v) Ishikawa, 67
<i>C. Nipponicum</i>	9		Tahara, 106 Ishikawa, 67 Winge, 114
<i>C. roseum</i>	9		Tahara, 106 Ishikawa, 67
<i>C. segetum</i>	9		Tahara (v) Ishikawa, 67
<i>C. indicum</i>	18		Tahara (v) Ishikawa, 67

TABLE XV (continued)

Species	Numbers		References
	Gametic	Somatic	
<i>C. Leucanthemum</i>	18		Tahara, 106 Ishikawa, 67 Winge, 114
<i>C. hakusanense</i>	27		Tahara (v) Ishikawa, 67
<i>C. morifolium</i> var. <i>genuinum</i> f. <i>japonicum</i>	27		Tahara, 106 Ishikawa, 67 Winge, 114
<i>C. Decaisneanum</i>	36		ditto
<i>C. arcticum</i>	45		ditto
<i>C. marginatum</i>	45		Tahara (v) Ishikawa, 67
<i>Matricaria ambigua</i>	9		Tahara (v) Ishikawa, 67
<i>M. Chamomilla</i>	9		Lundegardh, 74 Beer, 41 Ishikawa, 67 Winge, 114
<i>Centipeda orbicularis</i>	10		Ishikawa, 67
<i>Tanacetum vulgare</i>	9		Rosenberg, 89 Ishikawa, 66, 67 Winge, 114
INULEAE			
GNAPHALIINAE			
<i>Antennaria dioica</i>	12-14	24 ? 20 24-28 24	Juel, 69 Coulter and Chamberlain, 50 Gates, 57 Ishikawa, 67
<i>A. alpina</i>	12-14	45 ?-50 40-50 45-50 45-50	Juel, 69 Coulter and Chamberlain, 50 Gates, 57 Ishikawa, 66, 67
CYNARAE			
CARDUINAE			
<i>Saussurea affinis</i>	18		Ishikawa, 67
ASTERAE			
BELLIDINAE			
<i>Bellis perennis</i>	9		Ishikawa, 67 Winge, 114
HETEROCHROMINAE			
<i>Erigeron philadelphicus</i>	8	16	Land, 72 Ishikawa, 66, 67
<i>E. strigosus</i>	8	16	ditto
<i>E. dubius</i> var. <i>glabrata</i>	9		Tahara (v) Ishikawa, 67
<i>E. annuus</i>	13	26	Tahara, 107 Ishikawa, 67
<i>E. linifolius</i>	26		Tahara, 107 Ishikawa, 7
EUPATORIEAE			
AGERATINAE			
<i>Ageratum conyzoides</i>	10		Ishikawa, 67
<i>Eupatorium glandulosum</i>		49-52	Holmgren, 65
HELIANTHEAE			
MELAMPODIINAE			
<i>Silphium integrifolium</i>	8		Merrell, 77 Coulter and Chamberlain, 50 Ishikawa, 66, 67 Winge, 114
<i>S. laciniatum</i>	(8)	16	Land, 72 also 60, 66, 67, 114

TABLE XV (continued)

Species	Numbers		References
	Gametic	Somatic	
<i>S. terebinthinaceum</i>	8	16	Merrell, 77 Land, 72 Ishikawa, 66, 67 Winge, 114
AMBROSIINAE			
<i>Xanthium Strumarium</i>	18		Ishikawa, 67
ZINNIINAE			
<i>Zinnia elegans</i>	12		Ishikawa, 67
VERBESININAE			
<i>Wedelia prostrata</i>	15		Ishikawa, 67
<i>Helianthus annuus</i>	9		Tahara, 105 Ishikawa, 67 Bönicke, 43 Winge, 114
	16 ?		
COREOPOSIDINAE			
<i>Dahlia coronata</i>	16	32	Ishikawa, 66, 67 Gates, 57 Winge, 114
<i>D. variabilis</i>	32	64	ditto
<i>Dahlia</i> , garden varieties such as <i>D. Juarezii</i> and <i>D.</i> <i>gracilis</i> believed to be de- rived from <i>D. variabilis</i> and <i>D. coccineum</i>	32	64	Ishikawa, 66, 67

occurring in *Senecio*. As *Lactuca* has been suggested to be the primitive genus of the Cichorieæ, derived from the Senecioneæ, it is interesting to note that the most frequently occurring number in this genus is 5. In the same genus, *Lactuca*, both 8 and 9 occur also (cp. *Erigeron*), so it is clear that the number may vary in one genus between the various cardinal numbers, 5, 8, 9. This being so, the derivation of the various numbers from the primitive series may quite easily follow the derivation already suggested of the various tribes from the Senecioneæ.

The various types of hybridisation, especially the forms of philozygoty and pathozygoty distinguished by Winge (114, pp. 196-201), account for the variation in number *within* each of the three main series. The origin of the 8 and 9 series from the 5 series may be accounted for by the passing of $n-1$ chromosomes to one pole and of $n+1$ to the other, as observed by Winge (*loc. cit.*) in *Callitriche verna*. More unequal division of the chromosomes has been observed by Rosenberg (94) in *Hieracium*; the variations which he describes as semi-heterotypic include the migration of 3 gemini to one pole and 21 unpaired chromosomes to the other, and similar, very unequally balanced numbers.

C. LATEX IN THE COMPOSITÆ.

The phyletic value of the facts concerning the distribution of latex throughout the family and in the individual plants is considerable, but must always be subordinate to that of floral details. Col,

who has investigated the latex of the *Compositæ* more closely than any other author, clearly recognised this. He writes (120d, p. 155) "On juge en général de l'importance d'un caractère anatomique à sa constance dans une famille ou une tribu établie sur d'autres caractères ; cela n'est un moyen certain qu'autant que ces dernières, tirés le plus souvent des organes reproducteurs, ont valeur réelle."

The interpretation of these anatomical facts depends to a large extent on the theory which is adopted of the physiological function of latex and laticiferous tubes and vessels. Many theories have been given, such as the excretion theory of Treviranus, 1827, (see 124), who compared the laticiferous vessels with gum-resin canals. That latex is an excretion has been held by De Candolle (*Physiologie végétal*, 1832) and Richards (*Eléments de botanique*, 7th edit.). That latex is a secretion with a protective function has been held by Schimper (140), Groom (130), Tschirch (150), Kny (135), Czapek (120) and Sharples (142). The analogy of latex to the blood suggested by Schultz (1841) was developed by Trécul (146), who considered the laticiferous vessels to be "le système veineux" and the xylem vessels to be "le système artériel."

Many others have considered that latex has a nutritive function and is translocated, such as Treub (148), Biffen (117) who got positive experimental results for the translocation of sugar and proteid, Schwendener (141), Faivre (123, 125-6), Jussieu, Decaisne, Naudin, Hanstein (132), Schullerus, Haberlandt (131) and the writer (143). This theory is opposed by Schimper, Groom (130), Kniep (134), Leblois (136) and to a certain extent by Mangham (137).

Spence (145) considers that caoutchouc is a food reserve, rich in chemical energy, which is rendered available by oxydases, and he compares it with the glycogen in the liver which is broken down by glycolytic enzymes. The proteids are rendered available by proteolytic enzymes (127-8). That the laticiferous system has a dual function, nutritive and excretory, has been held by Sachs (*Physiol. of Plants*) and Faivre (124). Finally, a water-storage function has been suggested by Parkin (138).

The latex-containing elements in the *Compositæ* are cells, sacs or vessels. Comparisons in this family and in others, especially in the *Nymphæaceæ*, show that a series of transitions occur even in the same genus, from isolated, isodiametric cells containing latex through elongated, isolated, latex cells to sacs consisting of two or three elongated cells placed end to end, as in *Nuphar* and *Nelumbium*, or longer sacs consisting of numerous cells in long rows, as in *Brasenia* and *Cabomba* (144, Vol. I, pp. 48-9).

Numerous cases of transitions from such sacs to vessels are known; the vessels, indeed, frequently show the sac stage before the walls break down to produce the typical anastomosing system. Transitions between vessels and tubes are recorded for *Hevea* and *Manihot* (Euphorbiaceæ) and for *Tupa salicifolia* (Lobeliaceæ), cp. Trécul, 146, Tome VII, p. 178. Transitions from the common oleo-resin canals of the Compositæ to laticiferous vessels are recorded by Trécul (op. cit., p. 181) in *Gundelia Tournefortii* of which he remarks "Ces vaisseaux donnent donc un degré de transition de plus entre le canaux oléo-résineux des autres Composées et les laticifères les plus parfaits." See also 137a for somewhat similar canals in the primary and secondary phloem of *Rhus*.

Cells containing oleo-resins are so common in higher plants as excretory organs that the widespread occurrence of cells which also contain reserve proteid and carbohydrate does not call for any particular explanation.

The elongation of these cells and their organisation into sacs and vessels, with the extreme and peculiar case of the development of tubes instead of vessels, is best regarded as part of the epharmonic variation which produces climbing plants.

Before developing this suggestion it will be advisable to consider the function of laticiferous tissue in general. The oleo-resin cells are in the first place mere receptacles for excretory products; the same may be said of these cells as Record says of resin tracheids (139), i.e. they "represent one form of reservoir for excretions." The addition of reserve food material—proteid (129), etc., caoutchouc (145), carbohydrate, etc.—need not change or eliminate the excretory function. The second class of material is rendered available for immediate use by specific enzymes, which would separate the secretions from the excretions by solution and diffusion. The simple, isolated latex cell has, therefore, two functions; it is a receptacle for excretions and for food reserves.

The organisation of the cells into sacs produces no change in this duality of function. The food reserves still require to be dissolved before they can pass from one cell to another, from one part of the plant to another. The breaking down of the dividing walls when the sacs become vessels renders possible the translocation of the solid materials from one part of the vessel to another part of the same vessel no matter how distant it may be. That such translocation of solids does take place is considered proved for *Lactuca* by the preliminary experiments described by the writer (143). That translocation of sugars in solution takes place is proved for *Euphorbia* by Biffen's quantitative analysis of the sugar-

content of the latex in undarkened and darkened leaves (117). That both sugars and proteids are manufactured in the leaf and pass at once into the laticiferous vessels or tubes is rendered very probable by the above experiments, by the fact recorded by Biffen (*loc.cit.*) and others that the blind-endings of the laticiferous system are generally connected with the palisade cells of the chlorenchyma, and by the fact that in the Compositæ "it often happens that the laticiferous ducts are actual sieve tubes or are at least continuous with elements of that nature" (133, p. 433).

Laticiferous tubes can be considered as a special development of the vessels. The first stage is seen in *Tupa salicifolia*, where some of the cells comprising the vessel are branched.

The conclusion from the known facts is then that the tubes or vessels forming the laticiferous system exercise two functions; they are reservoirs for excretory products and at the same time are canals along which food materials can be easily and rapidly translocated to considerable distances either in solution or in the solid condition, and in which these same substances can also be stored until required.

If an explanation is sought for the development of this particular method of translocation in some groups of plants and not in others, the general prevalence of the climbing habit in those groups which show laticiferous tissue becomes significant. The four families in which laticiferous tubes occur, Euphorbiaceæ, Moraceæ, Apocynaceæ and Asclepiadaceæ, are well known to contain quite a number of climbing species. The same is true of many of the groups in which laticiferous vessels occur, *e.g.*, Araceæ, Convolvulaceæ, Lobelioideæ and Clusioideæ (*cp.* Trécul, 146). Other families which show laticiferous sacs or vessels, such as the Nymphæaceæ and Musaceæ, are herbs which develop long stems, petioles or peduncles by rapid growth. It is of interest to note also that in the Gymnosperms one of the few genera with many climbing species, *Gnetum*, has latex tubes in some species, *e.g.*, *G. africanum* (122) and *G. Gnemon* (119).

Oleo-resin or mucilage canals occur in a still larger number of families. The use of such canals by climbing plants or giant herbs for the translocation of food materials easily and quickly along stems where the cross section of the phloem is small compared with the size of the plant and the length of stem is just what might be expected. The writer, therefore, suggests that the development of the oleo-resin canals into a laticiferous system is part of the response to environment (epharmonic variation) which produces a climbing plant from an erect one. Such an advantageous character

would not readily be lost if the climber again developed the habit of an erect shrub or herb, especially if the phloem had become reduced in the interval. This would explain the relatively few cases, such as the Papaveraceæ and the non-climbers in the above mentioned groups, in which latex occurs in comparatively low-growing herbs or shrubs.

The present is not a suitable opportunity to develop this theory fully and we will proceed to apply it to the particular problem of the development of latex in the Compositæ. Laticiferous vessels and the climbing habit are concomitant characters in the *Siphocampylus-Centropogon* ancestors of *Senecio*. In that genus and in all the Senecioneæ which have been examined there is a system of oleo-resin ducts throughout the root, rhizome and aerial stem (see Fig. 77). The explanation of the absence of food materials from the canals in this case is to be found in the facts given in Chap. XI, C-D. It was shown there that the dominant feature of the evolution of *Senecio* from the *Siphocampylus* group must have been the dwarfing of the plant in an Andine habitat and the aggregation of all the aerial parts. This is the very opposite of the phenomena which, on the above theory of latex, lead to the development of a laticiferous system. In these circumstances it is not surprising that the duality of function ceases and the laticiferous vessels degenerate into oleo-resin ducts with only an excretory function. For this reason an examination of *Lysipomia* from the latex point of view would be very interesting. *Rhizocephalum* (another Andine genus) and *Apetahia*, the other two genera which show considerable reduction in the gynoeceum (cp. Chap. XI, C) have already been examined for latex with negative results (144 and 156). It is probable, therefore, that the change to oleo-resin canals had taken place during the dwarfing of the Andine plants before the origin of *Senecio*.

We thus arrive at a definite point of view with regard to the primitive condition of the secretory apparatus in the Compositæ: i.e., *Senecio*, being derived by a dwarfing process from the Lobelioideæ in which a laticiferous system extends to root, rhizome and aerial stem, has that system modified by the loss of its nutritive function into a series of oleo-resin canals, which also extends to rhizome and aerial stem.

Although many authors have contributed to our knowledge of the secretory apparatus of the Compositæ (see Faivre, 125-6, Kny 135, Triebel 149, Van Tieghem 151-3, Vuillemin 154-5, Leblois 136-Trécul 146-7 and Bibliography in Solereder 144) Col has given the

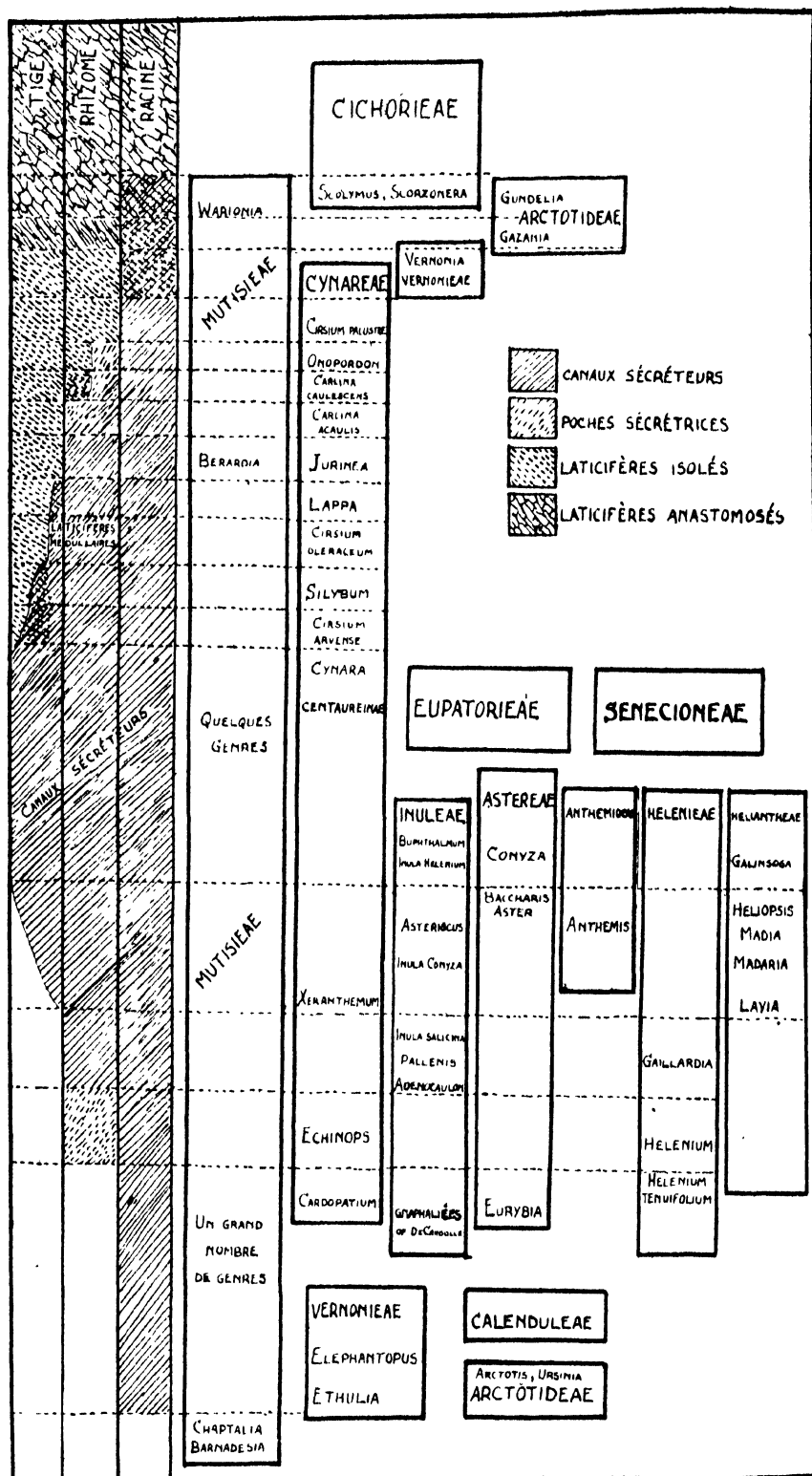


FIG. 77. Distribution of Secretory Tissue in the Compositae: modified from Col. For explanation, see text.

ences and he summarises the facts conveniently in a series of figures (120d). Fig. 77 is a copy of his Tab. II with some modification in the nomenclature and some additional genera added from his Tab. III. The three columns on the left indicate by the hatching, etc. the character of the secretory apparatus present in root, rhizome and aerial stem of the genera and groups on the right.

In his final contribution Col considers the phyletic value of the facts and gives two hypotheses for the development of the secretory canals in the Compositæ. According to the first the canals are in the process of disappearing completely or of being replaced by laticiferous elements. On this view he points out that the Senecioneæ and Astereæ are the primitive groups and the other tribes are grouped around them. According to the second the canals are in the process of appearing and in this case no primitive groups are indicated.

Although he says he prefers the latter hypothesis, he also states very definitely that he has given the tables and the two hypotheses "pour mettre . . . les taxinomistes futurs de tenir compte des données de l'appareil sécréteur interne de l'axe des Composées. Les affinités entre les groupes de cette famille sont si grandes, qu'il faudrait renoncer à une classification basée sur l'ensemble des caractères, avant de connaître d'une façon précise la valeur de ces caractères, et les causes de leurs variations." The problem is, therefore, quite an open one as far as Col is concerned, but in view of the preceding investigation of phylaxis in the Compositæ and the origin of the family from a group in which a secretory apparatus is fully developed, there can be no doubt that the first hypothesis is the correct one.

The facts are given in Fig. 77, and there is little that it is necessary to add, except that in the Senecioneæ and Astereæ the canals of the aerial stem are situated opposite the vascular bundles, are usually only feebly developed in or immediately within the endodermis, and are very similar to the simple canals of the rhizome. In all those cases, also, where canals of any kind are absent from a part of the aerial stem (as in *Asteriscus*, *Inula*, *Madia*) the canals which are present in the rest of the stem are situated at the sides of the vascular bundles. *Echinops* and *Helenium* have only sacs but they also are laterally placed. Further, the species in which the secretory tissue is present in the rhizome and entirely absent from the aerial stem belong to those tribes in which canals or sacs are lateral when present.

Considering Fig. 77, the Senecioneæ are again indicated as the primitive group. The Astereæ-Eupatorieæ line is quite clear, with

the advanced position of at least some of the *Heterochrominæ* (*Aster* and *Eurybia*) and of the *Baccharis* group confirmed. The

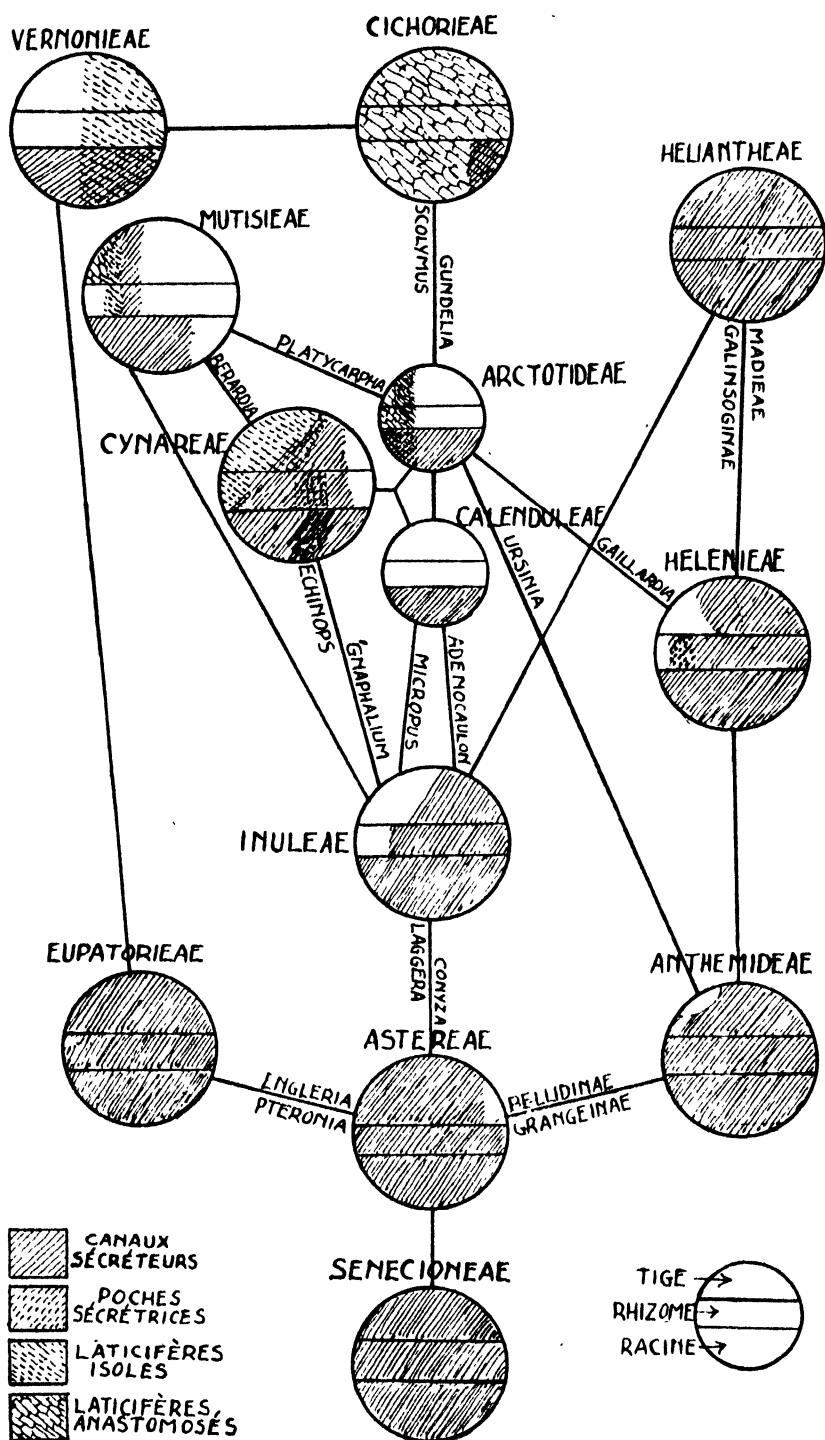


FIG. 78. Affinities among the Compositæ as shown by the distribution of secretory tissue; modified from Col.

position of the Anthemideæ, Heliantheæ and Heleniæ is in accordance with Fig. 7, except that a close affinity has again to be noted between the Senecioneæ and Heleniæ (cp. Chaps. V, D and X, D). The somewhat abrupt disappearance of the canals from the stem in the Calenduleæ and Arctotideæ (*Ursinia* and *Arctotis*) is not surprising when the variation in a single tribe (as in the Cynareæ, Mutisieæ, etc.) is observed.

In the Vernoniæ two distinct types occur; the appearance of laticiferous sacs in *Vernonia* may be correlated with the climbing habit of many of the species and a thorough examination of the climbing species of *Senecio* would be of interest in this connection. The derivative position of the Lychnophorinæ is confirmed by the total absence of secretory canals from the stem.

The distribution of the canals in the Inuleæ raises again the question of the monophyletic origin of that tribe. The "Gnaphaliées of De Candolle" includes the first seven sub-tribes of the Inuleæ of Bentham. The facts indicate a diphyletic origin, as suggested in Chaps. IV, F and VI, C. The variation in *Inula* would account for the distribution of the secretory apparatus in the Athrixiinæ and Relhaniinæ.

One of the most interesting points is that the secretory apparatus is equally developed in the Senecioneæ, *Inula*, *Helenium*, *Buphthalmum* and the Centaureinæ. The only difference is that in the first and last groups the canals are opposite the vascular bundles, while in the other two they are placed laterally or between the bundles. The origin of the Cynareæ from the Buphthalminæ thus receives confirmation. In *Cynara* and *Saussurea* (Carduinæ) the development of the canals is the same as in the Centaureinæ, so that the position of the Echinopsidinæ as derived from the Carduinæ (Figs. 7 and 77) is confirmed. The Carduinæ show a gradual development of laticiferous sacs possibly connected with the ecological conditions which have played so conspicuous a part in the development of the Cynareæ, (cp. Col's conclusion from his experiments that the environment determines the appearance of the secretory organs in some Compositæ but not in others (120d, p. 164). The change in the case of the Cynareæ would be rendered easy by the ancestral laticiferous characters, which, although suppressed, do not appear to have been completely lost. The Carlininæ show a wide range from *Carlina acanthifolia* with anastomosing laticiferous vessels to *C. caulescens*, *Xeranthemum* and *Cardopatum*. This is in accordance with the derivation of this sub-tribe from the Carduinæ (Fig. 7),

the *Carlina* group corresponding to the *Cirsium* line and the *Xeranthemum* group corresponding to the *Echinopsidinæ*.

The somewhat anomalous genera, *Warionia* and *Berardia*, were removed from the *Carduinæ* of Bentham and placed in the *Mutisieæ* by Hoffmann, for reasons which are not given but may be found in Bentham's note on the latter genus (I, 8, p. 474). Although he was not quite certain about the position of these two genera, Bentham's opinion as expressed in his classification is to be preferred to Hoffmann's, who seems to have followed on more than one occasion the former's suggestions of alternative affinities with no further evidence or reason. The *Mutisieæ* can, therefore, be regarded as a more or less homogeneous group as far as the secretory canals are concerned. The tribe shows a clear gradation from genera similar to the *Senecioneæ* to the extreme cases of *Chaptalia* and *Barnadesia*.

Considering the fact that reversion to the ancestral condition is shown in the *Cynareæ*, the appearance of laticiferous vessels or sacs in *Gundelia* and *Gazania* (*Arctotideæ*) may be taken as confirming the derivative position of the *Gundeliinæ* and *Gorteriinæ* (cp. Fig. 7).

The *Cichorieæ* have the laticiferous system well developed; the only genera which show oleo-resin canals in the root are *Scolymus* and *Scorzonera*. In Chap. VII, C, it was suggested that the receptacular paleæ are atavistic; the *Cichorieæ* also show reversion to their Lobelioid ancestors in the posterior split of the corolla. This atavism is easily understood if the tribe is closely related to the *Senecioneæ*. There is then only one step between the *Lobelioideæ* and the *Cichorieæ*, so that reversion should be comparatively easy. This close affinity, combined probably with the environment at the time of the origin of tribe, explains the reversion of the *Cichorieæ* in the secretory apparatus as well as in the corolla and receptacle.

Col gives a figure (120d, Tab. IV) representing "sur un plan la terminaison de l'arbre généalogique de la famille de Composées," in which he indicates affinities as shown by radiate capitula, presence of receptacular paleæ and tailed anthers, in addition to the characters of the secretory apparatus. As his treatment of the first three characters is somewhat superficial and inaccurate, it has been omitted from Fig. 78, which is a reproduction of Col's Tab. IV, modified to occupy less space but with the affinities as indicated by that author.

Although this (Fig. 78) is considered to represent the ends of the phyletic lines, the capitula of the corymb so to speak, several of

the affinities which have been considered in previous chapters can be traced.

As shown above, however, much more evidence can be adduced in favour of the phylesis as expressed in Fig. 7, Chap. II, and modified in subsequent chapters. The facts concerning the secretory apparatus are not only in agreement with the general lines of evolution but confirm a number of detailed affinities in a very interesting fashion. As this conclusion is arrived at by the use of the theory of latex outlined above it serves as a confirmation of the usefulness of such a theory, if not also of its actual truth.

In spite of the extensive work by Col and others on latex in the Compositæ, much remains to be done as our knowledge is still incomplete. This fact is well illustrated by the recent description (116) of latex sacs in a species of *Parthenium* (Melampodiinæ), one of the advanced Heliantheæ, in which latex is present in sufficient quantity to be of possible commercial value as a source of Guayule rubber. Another source of rubber is *Hymenoxys floribunda* (Heleniinæ) but the quality is said to be inferior (see 119a).

D. SOME ISOLATED DATA.

There remain to be considered some isolated data referring to morphological and physiological characters which are of minor importance or which do not extend to a representative number of genera and tribes.

Seedling Structure.

The work of Dufour (I, 26) and Lebard (I, 53), which was mentioned in Chapter I, is now of more interest. Lebard derived the Cichorieæ from the "Tubuliflores" through the genera with long, narrow cotyledons, the Leptocotylées of Dufour. The examination of an extensive and representative collection of seedlings grown for the purpose shows that the broad cotyledon is the predominant type throughout the Tubulifloræ; it may be long or short but only in a minority of genera do we find the long cotyledon also linear and in still fewer is the short cotyledon at all narrow. Lubbock (167) considered that "One of the simplest types of embryo is that seen in the species of *Senecio*," where the cotyledons are short and oblong-obovate.

Lee's work (I, 54) on the seedling anatomy of the Compositæ led him to the conclusion that such data are of no use in questions of affinity. There is a marked divergence of opinion on the primitive type of root, diarch or tetrarch (cp. Thomas, 170). Only one type of transition with variations occurred in the fifty species of Compositæ examined; these were all diarch or tetrarch and showed variations between these extremes in nearly related species or

in different examples of the same species. This is only to be expected after Compton's proofs (160) that in the Leguminosæ the type of vascular anatomy in the seedling is correlated with the size of the latter. Hill and de Fraine (164), using examples from the Compositæ and other families, found that the area of the cross-section of the vascular bundles in the seedlings is correlated with the surface area of the cotyledons. Lee (*loc. cit.*) found that in the Compositæ there are also variations which cannot be correlated with any external factors or characters.

The cause of much of the variation in the anatomy of the seedling is thrown a step further back by Lubbock (*op. cit.*, p. 102), who says "The prevailing type of the cotyledons in the seedling stage is spathulate, a shape due to that of the seed, which in turn strictly conforms to the interior of the fruit." The shape of the fruit clearly depends on the conditions under which it matures, for example, the fruits in the centre of the capitulum of most thistles are quite straight, but those around the outside are curved and have the pappus inserted obliquely. The narrow fruits of *Scorzonera* and *Tragopogon* mature on a flat receptacle, while enclosed by a long, rigid involucre. The result is the long, narrow cotyledon characteristic of these genera. In other genera where the fruits have more room to expand radially instead of longitudinally the short, broad type of cotyledon results.

In the seedling, as in the embryo, *Senecio* shows the primitive type, and Lebard's scheme (Table IV, Chap. I) must be reversed. This brings the genus *Lactuca* into the primitive group of the Cichoriæ and the scheme, with some modification, is then in accordance with the views on the evolution of the Cichoriæ given in Chap. X. With the *Senecio* or *Lactuca* type as primitive the variation in the other tribes, although in most cases considerable, is in accordance with the general lines of phylesis as deduced from other data.

Pericarp.

Various authors (61, p. 283; 169, 172, etc.) have investigated the detailed structure of the ovule, but Laviolle's extensive work on the pericarp is the only one which yields interesting phyletic data. His conclusions are given in Fig. 3, Chap. I, and are of interest as far as the Cynareæ are concerned. The Centaureinæ and Carduinæ appear as a large basal group from which the Carlininæ are given off, with *Atractylis* as an intermediate genus and *Xeranthemum* connecting with the Mutisiæ. The Echinopsidinæ are given as derived from the Carlininæ (cp. Figs. 7 and 79).

Anatomy.

The general anatomical characters of the Compositæ are of little use in classification of groups above the rank of genera (cp. Vuillemin and Hildebrandt, Chap. I, B, also Michael, 168), but a critical analysis of the facts might well lead to the elucidation of evolutionary principles, if the main lines as laid down in Chapter XIII and Fig. 79 were taken for guidance.

An interesting point is mentioned by Whitaker (173), namely, the occurrence of internal phloem in the leaf traces as they pass through the cortex; this is figured for *Solidago* and mentioned as a general feature "of the genus and probably of the family." Various types of phloem development have been observed in these leaf traces; it may be all round the xylem, as it is sometimes in *Olearia Haastii*, or almost completely encircling the xylem, as in some species of *Senecio*, or of the bicollateral type, as in other species of *Senecio*. These facts are of interest on account of the bicollateral bundles of the Cucurbitaceæ, one of the lowest families of the Campanulata. For other anatomical anomalies, such as "inverted" bundles, medullary bundles, etc., the reader is referred to Solereder (144) and the papers there mentioned.

Phytochemistry.

Systematic phytochemistry is a subject which must be largely developed in the future if there is to be any rational exploitation of plants. Hallier (163) deals with it in a general exposition of what is known and Greshoff (162) makes a strong plea for this eminently utilitarian study. Comparative phytochemistry is sometimes of distinct value in cases of doubtful affinity (cp. 163 and X, 39), and if the subject were properly developed it would at least remove the stigma from science which results from the fact that up to the present our knowledge of the medicinal properties of plants rests, in practically every case, on the experience of savages or barbarians. Only in a very few cases has civilised man discovered a new medicinal plant, either in his own or in any other country.

The literature of the subject, so far as the Compositæ are concerned, is so scattered through chemical and pharmaceutical publications that only one or two interesting points can be noticed here. The subject awaits a proper systematic investigation both practically and bibliographically.

The medicinal properties of the Compositæ are discussed in a general way by Lindley (I. 56, pp. 199-201). Greshoff (*loc. cit.*) records the occurrence of cyanogenetic glucosides in a number of genera, notably in the Cynareæ and Anthemideæ, also of saponin in a smaller number of genera. Two alkaloids, senecionine and

senecine, are recorded for *Senecio vulgaris* (161). The intimate relationship of *Senecio* and *Ligularia* is emphasised by the occurrence of senecioic acid in *Ligularia tussilaginea* (157), while the less close relationship of *Arnica* and *Tussilago* is confirmed by the occurrence in the latter of faradiol, a bivalent dextrophytosterol closely related to arnidiol, a constituent of *Arnica* (165-166).

Many of the constituents of the latex, oleo-resins and gum-resins have a commercial value, but the most interesting case is *Stevia Rebaudiana*, the dried, powdered leaf of which is 40-50 times sweeter than any other natural product and can be used in the crude condition as a non-toxic substitute for saccharin. The sweet constituent is a glucoside, estevin or eupatorin, and the sweetening power of the pure substance is 150-180 times that of cane-sugar (see 171 for review of facts and literature).

Much more is known of the chemical constituents of the Compositæ but much more still remains to be added before the facts can be used in a rational manner, either in the investigation of phylaxis or in the utilisation of the plant products for economic purposes.

Pappus.

Since Chapter V was written some adverse criticism has been made of the views there expressed on the trichome nature of the pappus. Further evidence has arrived also, which supports the trichome theory in a very interesting way. As no decided opinion on the fundamental nature of the pappus was expressed in the previous account, the issue will now be made clear. The present writer holds that the pappus is a trichome structure or an emergence and not a divided calyx, for the following reasons:—

(1). The structure of the mature pappus, even in the paleaceous forms, is that of a series of hairs which have become fused throughout all or part of their length, either side by side to give a scale or in a mass to give a seta or awn.

(2). The development of the members of the pappus is either that of a typical trichome or that of an emergence, such as the surface spine of the thistle-leaf, which is comparable with some of those anomalous cases in which vascular bundles have been found in the pappus.

(3). The primitiveness of the scabrid seta is in conformity with the evolution of the family as deduced from other data.

(4). The predominant type of pappus in the fossil forms is the setose type. No fossil foliose pappus is known.

(5). The similarity of the setæ to the achenial hairs is very marked. In the primitive genus the latter are already biseriate and

have a bicellular pulvinus (Fig. 11, Chap. V) which causes the hairs to diverge in moist conditions; the former are pauciseriate and have a pulvinus which causes the setæ to diverge in dry conditions. This difference in the action of the pulvinus may be due to the position of the setæ on the top of the pericarp and in any case is probably epharmonic.

(6). Blake has pointed out (159, p. 6) the general concomitance of the presence of pappus and the presence of achenial hairs or the absence of pappus and the absence of achenial hairs. This "pair of linked characters (pappus and pubescence of the achene)." is used by Blake (*op. cit.*, p. 48) to separate two varieties of *Viguiera flava*, which are "sometimes growing together and not separable by any other character." An extensive examination shows that the linkage of these two characters is very common throughout the Compositæ in tribes, genera, species, varieties and forms. There are a few exceptions but the great predominance of the linkage is sufficient to render it almost, if not quite, certain that the two characters are inherited together. As they apparently behave as one character, there seems to be no real reason why they should be regarded as two distinct units in the genetic constitution of the plants. One systematist aptly summarised the point, when he said that "one could not properly describe a pappose achene as glabrous."

Since there is no conceivable reason why the character of a free calyx-limb should be linked with the character of pubescence of the achene, this new point is regarded as decisive.

The teratological specimens of Treub (V, 66) and Worsdell, (IV, 96) are properly explained by Buchenau's observations (see Chap. V, A) of a pappus inserted upon five green leaflets, which were developed in inverse proportion to the pappus. As the true sepal aborts the hairs upon it become larger until they are the only structures left. In this sense only can the pappus be regarded as a reduced calyx. This would also account for the occasional grouping of the setæ in five more or less obscure bundles and the subsequent fusion of these bundles of setæ to give five awns or paleæ.

Pubescence of the sepals is very frequently linked with pubescence of neighbouring parts such as the pericarp, the outer layers of which may be formed in the Compositæ from the fused calyx tube. Another point in favour of this view is that where hairs occur on the corolla they may be organised into a pappus as in *Leontopodium* (cp. Worsdell, IV, 95, p. 77 and Chap. V, A).

Since all the facts adduced in support of the phyllome theory can

be easily and adequately explained by assuming that the pappus is in part, at least, a development of the hairs which were inserted on the now aborted free calyx segments, the evidence in favour of the trichome or emergence nature of the organ admits of no other conclusion regarding the origin and essential homologies of the pappus.

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CHAPTER XIII.

GENERAL CONCLUSIONS.

THE results of the present investigation of the Compositæ are chiefly of two kinds; the phylaxis of the family and of its chief groups has been elucidated, and various theories have been given to account for the origin and development of the structures and physiological and cytological phenomena which occur in the family. The historical evolution of the tribes is discussed briefly in the first chapter, together with previous phylogenetic suggestions. As these suggestions were in most cases based upon only one or a few characters it is unnecessary to discuss them in detail. It will be sufficient to point out that the affinities of the tribes suggested in the present account have almost all been recognised by previous synantherologists.

The results of general importance are summarised below.

Styles and Stamens. The evolution and biological significance of the appendages of the styles and stamens have been elucidated and the general economy-tendency has been shown to extend to the polliniferous tissue. The two general principles, "the progressive sterilisation of potentially sporogenous tissue" and the elaboration of the sterilised tissue, are exemplified in the evolution of the anther appendages.

Irritability of the Stamens. Our knowledge of thigmotropism of the stamens has been extended to all the tribes, except the Eupatorieæ and Vernoniæ, and to most of the sub-tribes of the family. Subsidiary results of the investigation of irritability are the new record of thigmotropism in the style of *Guzania splendens*, the differentiation of five types of movement of the stamens, and the theory of the differential changes in the permeability of the cells of the filaments as the cause of the movement.

Corolla. The ray florets are shown to be essentially bilabiate in development and structure, and the occurrence of inner rows of ray florets is shown to be related to the food-supply of the capitulum. Other results of the investigation of the corolla are the elucidation of the evolution of colour in the family from yellow, through orange and white, to red, purple, violet and blue, and the recognition of the filiform corolla as a reduced type.

Pappus. The setose pappus is proved to be primitive by its mature structure (Chap. V), by the presence of a pulvinus, by its development in the individual and in the family, by its common occurrence in the earlier known fossil Compositæ, and by the correlation between pubescence of the achene and presence of pappus (Chap. XII, D). Subsidiary results of the investigation of the pappus are a re-affirmation with new evidence of its trichome nature, and the elucidation of the evolution of the various types from the scabrid setæ by fusion and reduction, two tendencies which are recognised as general in the other parts of the flower and inflorescence of the family.

Origin of the Capitulum. The development of the capitulum is shown to be due to the abortion of the pedicels in a racemose umbel rather than the non-elongation of the main axis of a spike. All the essential characters of the capitulum are explained by this theory.

Involucre. Two parts are differentiated in the involucre, the pericline and the calyculus. The primitive involucre is shown to be one with an uniseriate pericline and a slightly developed calyculus. This is confirmed by the structure of the earliest known fossil involucre.

Receptacle. The receptacular alveoles and setæ are shown to be new outgrowths, and the detailed structure and distribution in the family of these and other receptacular appendages are explained. The paleæ of the receptacle are regarded as atavistic to a pre-Composite ancestor when they subtend the florets, and as a development of the flimbrillate type of appendage where, as in the Cynaræ, they do not subtend the florets.

Phyllotaxis. The pericline and calyculus are shown to be distinct structures; the pericline is the row of members transitional between the curve-system of the cauline leaves or calyculus and the curve-system of the disc florets. These transitional members subtend the ray florets in radiate capitula. The pericline is, therefore, primitively uniseriate. Other results of the

investigation of the phyllotaxis are the proof of the primitiveness in the family of alternate phyllotaxis in the cauline leaves, and the elucidation by Church's work of the rules governing the number of rays and the general symmetry of the capitulum.

Fruit Dispersal. Winds of comparatively small velocities are proved to be sufficient to disperse pappose fruits to any distance under proper conditions of atmospheric humidity. A method and a formula¹ are given for calculating from the rate of fall in quiet air the minimum wind necessary for the dispersal of pappose fruits. A new type of anemometer of considerable accuracy is described. New experimental methods for determining the rate of fall in quiet air and the minimum wind necessary for dispersal are given. The hydrodynamics of the wind-dispersal of pappose fruits are elucidated.

A preliminary explanation is given of the general phenomenon of the elongation of the stalk of the fruit or spore-sac which in most cases immediately precedes fruit- or spore-dispersal. This explanation is also applicable to the elongations of the axis which take place in the female cone of *Pinus*.

Geographical Distribution. The previous phyletic conclusions and the validity of the Law of Age and Area are confirmed by the geographical distribution of the species, genera and tribes of the family. The principle of physiological differentiation and restriction of area is elucidated. Other points illustrated are the irreversibility of evolution, the development of peculiar types in each well-defined climatic region, the correlation between ecological conditions and the vegetative forms assumed in the various tribes, and the existence of definite centres of origin and paths of migration for the various tribes.

The explanation (Chap. X, A) of the espalier and cushion forms of plants by permeability changes which are directly due to the environment is of particular interest, since this view of epharmosis is capable of extensive development both experimentally and theoretically (cp. Chap. III, D, and Bib. III, 49-50, and X, 68a).

Origin of the Compositæ. It is shown to be highly probable that *Senecio* originated from the *Lobelioidæ* by orthogenetic saltation and epharmosis in late Cretaceous or early Tertiary times in a particular region of South America. An eclectic theory of evolution is suggested and a close analogy is traced between orthogenetic saltation and the disintegration process of the radioactive elements.

¹ See footnote on page 178.

Fossil Compositæ. A list is given of most, if not all, known fossil Compositæ. The occurrence of the various types of fossil Compositæ fruits is shown to be in accordance with the phyletic suggestions in previous chapters.

Cytology. Considering relationships within the family, the chromosome number is shown to be of some phyletic value. The development and type of haustorial antipodals also agree with previous phyletic suggestions.

Latex. A general theory is given of the evolution and functions of laticiferous tissues; the functions are excretory and nutritive; the evolution is suggested to be the result of epharmonic adaptation to a climbing or rapidly-elongating habit, which requires the easy and rapid translocation of food materials obtained by the development of a laticiferous system.

These are the general results, as distinguished from the phyletic results, which will now be discussed for each tribe.

PHYLETIC CONCLUSIONS.

Senecioneæ. The main thesis of the preceding chapters is that *Senecio* was the first genus of the Compositæ to come into existence and that it has directly or indirectly given rise to all the other genera of the family. That *Senecio* is the basal genus of the Compositæ is a theory which is supported by all the details of its vegetative and floral morphology, physiology and cytology, *i.e.*, the chromosome number, the antipodal haustorium, the anomalous septa and lateral placentæ in the ovary, the simple structure of the seed and seedling, the simple appendages of the styles and stamens, the simplicity of the pollen-presentation mechanism as a whole, the simple type of irritability of that mechanism, the numerous species and varieties with discoid capitula, the variation in form, development, colour and vascular anatomy of the corolla, the setose-scabrid pappus, the pulvinate achenial hairs, the small, flat, simple receptacle, the uniseriate pericline, the slightly developed calyculus, the alternate phyllotaxis of the cauline leaves, the development and contents of the secretory system, and the extreme plasticity of vegetative organisation or low physiological differentiation as shown by the marked response to a variety of ecological conditions. This theory is also confirmed by the geographical distribution of the genus and its close approach in the details of floral structure to the ancestral genera in the Lobelioideæ. The 2500 species of *Senecio*, constituting 10% of the Compositæ, form a very substantial "trunk" for the family tree (Fig. 79).

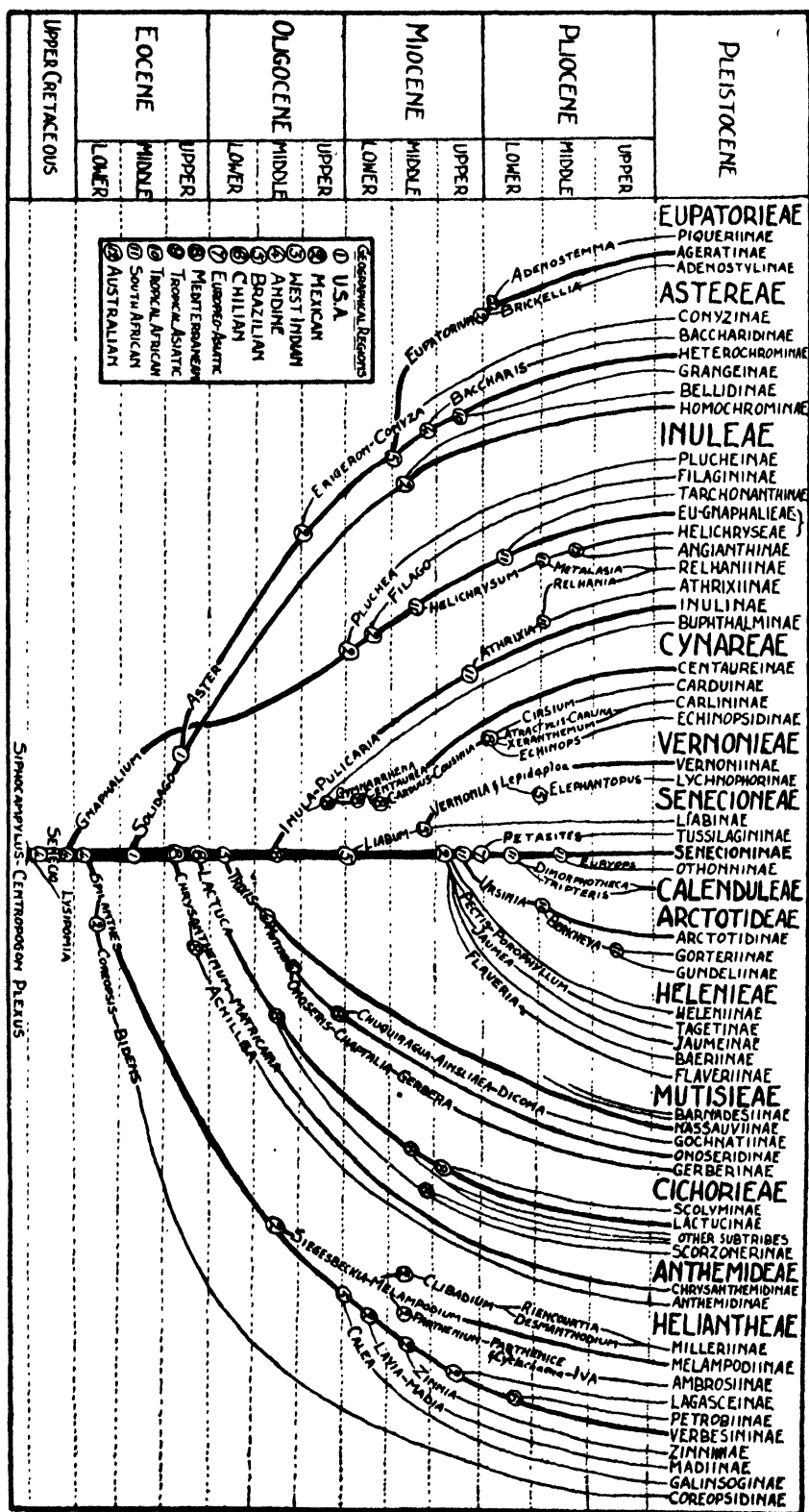


FIG. 79. The Evolution of the Compositæ in Time and Space.

The origin of *Senecio* from the *Siphocampylus-Centropogon* group of the Lobelioideæ somewhere between the forests of the Amazons and the heights of the Andes has been proved as clearly as is possible without actual ocular demonstration of the process. The evolutionary processes involved in this origin are shown to be orthogenetic saltation and epharmosis, and the date of the event is indicated by the geological evidence to be the late Cretaceous Period and approximately the same as the date of the first upheaval of the Andes.

The Senecioninæ consist of a group of genera closely related to *Senecio*. The detailed evolution of the genera in this sub-tribe is interesting, but is reserved, together with the detailed generic evolution of the other tribes, for future contributions. The facts of floral morphology and geographical distribution which are available should be supplemented by other data before any attempt is made to deal with the details of phyletic in the smaller subdivisions of the family. It will be sufficient for the present to suggest possible basal or transitional genera where these are clearly indicated.

Liabum is the primitive genus of the Liabinæ; this is shown by the floral morphology and geographical distribution. This genus may be regarded as the *Gynura* of America, the type VIIa style of *Gynura* being very similar to the type III style of *Liabum*; other characters also show a parallelism. It is interesting to note that these two genera flourish in the same latitudes, the one in America and the other in the Old World. The transition from the discoid species of *Liabum* to *Vernonia* is more a matter of the corolla colour and the phyllotaxis of the cauline leaves than anything more serious.

In Chapter II, E, the very close proximity of one genus of the Tussilagininæ, *Cremanthodium*, to *Senecio* is discussed. This sub-tribe is probably not monophyletic in the sense that a single primitive genus in the group has given rise directly or indirectly to the other genera; it is probably monophyletic in the sense that all the primitive genera have arisen directly from *Senecio*. Thus *Cremanthodium* is a comparatively recent genus which has arisen directly from the *Ligularia* section of *Senecio*. It is very probable, although less certain, that *Petasites* also arose in the same Asiatic region, but at an earlier date, from *Senecio* and *Ligularia*, and that it has given rise to the other genera of the Tussilagininæ. *Alciope* in South Africa is probably a third offshoot from *Senecio*. The

derivation of this sub-tribe from the *Ligularia* type of *Senecio* is confirmed by the floral morphology, by the general habit and by the slight or slow irritability of the stamens or its complete absence in that type of *Senecio*.

Apart from *Werneria*, which is possibly a polyphyletic genus, the Othonninæ are clearly of recent South African origin, with *Euryops* as a probable primitive genus. *Euryops* is distinguished from *Senecio* only by its fused periclinal bracts and the wavy setæ of the pappus. The Othonninæ are also connected with *Senecio* through *Othonna* and *Othonnopsis*, but the differences are greater along that line, and although *Othonna* has more species than *Euryops* the area occupied by the latter genus is greater.

Cichoriæ. The derivation of the Cichoriæ from the Senecionæ involves very few changes of any magnitude. The pollen-presentation mechanism is of a simple type; the peculiar folding of the exine is approached in *Senecio vulgaris*; the homogamous, non-radiate capitulum is similar to the discoid species of *Senecio*; the predominance of yellow as a corolla colour and the simpler types of pappus which occur are other characters which show the affinity; still others are the simple, small, almost flat receptacle, the uniseriate pericline with or without a slightly developed calyculus, and the alternate phyllotaxis of the cauline leaves. The occasional occurrence of receptacular paleæ is to be considered a reversion to a pre-Composite ancestor. The posterior split of the corolla and the development of laticiferous vessels are the two chief changes and these also are clearly of the nature of reversions to the Lobelioid ancestors of the Senecionæ.

The sub-tribes are rather artificial, but we can distinguish the *Lactuca-Sonchus* group as primitive and the *Scorzonera* group as advanced. *Lactuca* is indicated as the primitive genus by all the characters of the florets and inflorescence, the seeds and seedlings, the chromosome numbers, and the geographical distribution.

The time and place of origin of the tribe are both clearly shown; the centre of origin is shown to be the Mediterranean region by the present geographical distribution; the occurrence of the *Lactuca* type and other Cichoriaceous material in the Lower Oligocene of Aix-en-Provence is in accordance with this conclusion and at the same time gives the date of origin as that period or a little earlier.

Calenduleæ. The Calenduleæ are closely allied to the Senecionæ in the structure of the styles and stamens, in the

irritability of the stamens, in the colour and anatomy of the corolla, in the simple receptacle and involucre and in the phyllotaxis of the cauline leaves. The chief differences are the usual absence of pappus and the usual heteromorphy of the achenes. It is not surprising, therefore, that Bentham wrote (I, 7, p. 463) that the *Calenduleæ* "might almost have been enumerated amongst the subtribes of the *Senecionideæ*." *Dimorphotheca*, with type IV style, type 4 or type 10 stamens, disc florets sometimes fertile, no pappus, plain receptacle, simple involucre and alternate phyllotaxis, is indicated as the primitive genus, but *Tripteris* is almost equally primitive; it has the disc florets always sterile and occasionally opposite phyllotaxis, but the pappus is coroniform and the involucre is very simple; it also has a wider geographical area. It is practically certain that the tribe is polyphyletic on account of the Chilean genus *Eriachanum*, and it is quite probable that the remainder of the group is at least diphyletic, if it is not only a mere collection of African *Senecioneæ* with heteromorphous achenes.

The place of origin is clearly South Africa and in the complete absence of fossil evidence the date may be taken as quite recent, probably Pliocene.

Arctotideæ. This tribe is separated from the *Senecioneæ* by a number of characters, such as the type of style, pappus, receptacle and involucre. The primitive genus, *Ursinia*, with the widest geographical area, is more closely related to the *Senecioneæ* than any of the other genera. *Ursinia* has the *Senecio* type of style and stamens, shows no irritability of the style and has yellow as the predominant corolla colour. The paleæ of the pappus and receptacle are comparatively advanced features, but are secondary to the inner floral characters. *Berkheya* by its floral structure and geographical distribution is indicated as the primitive genus of the *Gorteriinæ*, which sub-tribe has the *Gundeliinæ* as a small, possibly diphyletic, off-shoot.

The place of origin of the tribe is clearly South Africa and the date is probably a little earlier than that of the origin of the *Calenduleæ*: considering the extension of the tribe into Australia it is probably lower Pliocene.

Anthemideæ. In the pollen-presentation mechanism the *Anthemideæ* are very similar to the *Senecioneæ*, except for the type V style of the sterile florets. The corolla colour is higher and the chief differences are the almost complete absence of any pappus except the reduced, paleaceous coroniform type, and the scarious

margins of the involucre bracts. The epaleaceous receptacle and geographical distribution indicate the Chrysanthemidinae as the primitive sub-tribe, while these characters and those of the florets indicate *Chrysanthemum* as the primitive genus with *Matricaria* as more or less contemporaneous in origin. If *C. segetum* is carefully compared with a radiate *Senecio* with the calyculus well developed only the two chief tribal characters and general habit are found to distinguish the two types, and *C. segetum* has a fairly extensive geographical area.

Achillea is indicated by its floral characters and geographical distribution as the basal genus of the Anthemidinae, the chief difference being the paleaceous receptacle, which here, as in the Cichorieae, is considered to be an atavistic character. That it occurs in both cases in genera which are advanced in other characters is confirmation of the reversionary nature of this type of receptacular appendage.

The place of origin of the tribe is shown by the present geographical distribution to be the Mediterranean region. The date of origin is indicated by the same facts to be earlier than that of the Cichorieae. The presence of the *Chrysanthemum*-like leaves of *Parthenites priscus* in the Mediterranean region in the lower Oligocene, and the occurrence of the Anthemidean type of pappus and achene (*Hyoserites Schultzei*) in the Upper Miocene in another locality of the same region confirm, as far as is possible with our present knowledge, both time and place of origin. The *Cypselites trisulcatus* of the lower Oligocene has certain resemblances to the achenes of the Anthemideae and it is possible that further investigation may show that those epappose achenes have in most cases been passed over on account of the absence of the pappus.

Inuleae. Throughout the analysis of the various characters of this tribe there has been some difficulty on account of the synthetic nature of the group. The diphyletic origin suggested by the filiform or bilabiate outer florets is confirmed by the structure of the involucre, the haustorial development of the antipodals, the secretory apparatus and the geographical distribution.

If Tables VI and VII are examined in the light of these suggestions various points can be seen. In Table VI the Tarchonanthinae can be neglected as a small, special group. The other four sub-tribes with a filiform corolla (Pluchinae, Filagininae, Gnaphaliinae and Angianthinae) show a large proportion of type IV styles; type XIII styles are also well represented in the "filiform"

sub-tribes. In the last three sub-tribes (*Athrixiinæ*, *Inulinæ* and *Bupthalthinæ*) type XII is the dominant form of style. The *Relhaniinæ* show an exceptional proportion of type IV styles for a radiate sub-tribe.

Turning now to Table VII it will be noted that with one exception all the genera showing the simpler types of stamens occur in the "filiform" group, the first five sub-tribes. The predominance of type 10 stamens in the *Gnaphaliinæ* and *Inulinæ* mark these sub-tribes as the primitive groups of the two divisions of the *Inuleæ*. The four chief types of stamens in the tribe are 10, 12, 13, 14. All four types occur in the two basal sub-tribes and among the other sub-tribes only in the *Relhaniinæ*. A more detailed examination of the floral characters of the *Relhaniinæ* shows that sub-tribe to be a mixture of genera, some with radiate capitula and others with few-flowered, homogamous capitula. A diphyletic origin of this sub-tribe is clearly indicated, one line coming from the *Helichryseæ* with *Metalasia* as the primitive genus, the other coming from the *Athrixiinæ* with *Relhania* as the primitive genus.

In the *Inuleæ*, therefore, we have two main phyletic lines. The first line begins in the *Eugnaphalieæ* with a South American origin from the *Senecioneæ* at an early date and passes to the *Filaginæ* with a Mediterranean centre of origin, the *Plucheinæ* with a tropical African centre, the *Helichryseæ*, *Tarchonanthinæ* and part of the *Relhaniinæ* with their centres in South Africa, and finally to the Australian *Angianthinæ*. The second line begins with the *Inuleæ*, originating from the *Senecioneæ* at a later date than the *Eugnaphalieæ* in the Mediterranean region, and passes in the same region to the *Bupthalthinæ* and in South Africa to the *Athrixiinæ* and the rest of the *Relhaniinæ*. This development harmonises with all the known characters of the groups, including the geographical distribution, and exemplifies the parallel evolution, polyphyly and convergence which are discussed in Chap. XI, B.

In Fig. 7 the *Helichryseæ* are shewn as preceding the *Eugnaphalieæ*, but the geographical distribution indicates and the other data on more critical analysis confirm the view that the latter group is the primitive one for the "filiform" sub-tribes of the *Inuleæ*. Beauverd (XII, 158) places *Helichrysum* before *Gnaphalium* when he gives the chief genera of the sub-tribe "dans l'ordre évolutif présumé." He, however, used the fertility or sterility of the flowers as his chief guide and the work of Uexküll-Gyllenband (II, 69) shows that this cannot be taken as of primary importance

in phylesis; it is also proved by the fact that the other characters which are analysed by Beauverd do not follow the same sequence as the homogamy or heterogamy of the capitulum.

The data available for the determination of the times of origin of the two main lines are confined to the probable origin of the Senecioneæ in the Upper Cretaceous, the known development of the Cynareæ in the Upper Miocene and the present geographical distribution of all the groups concerned. From these data, however, the date of the first development of the Eu-gnaphalieæ can be placed soon after the origin of *Senecio*, probably early Eocene; and the date of the origin of the Inulinæ must have been later than that but some time before the Upper Miocene. Taking all the facts into consideration the date indicated is the middle Oligocene. Such a date would account for the absence of the Cynareæ from the lower Oligocene and would also give a sufficient interval for the development of the *Arctium* type of the Cynareæ in the Upper Miocene (see below under Cynareæ). At the same time it would account for the similarity in the present distribution of the Inulinæ and Cichorieæ, as well as for the greater area occupied by the latter, which is the older group.

Cynareæ. Two possible sources, the Plucheinæ and Buphthalminæ, have been suggested for the Cynareæ and a diphyletic origin of the tribe has been indicated as a possibility. As diphylesis is supported only by the evidence from the pappus it will be neglected until a more detailed examination has been made of the evolution in the tribe. The rest of the characters, including the geographical distribution and the secretory apparatus, support a monophyletic origin of the tribe from the Inuleæ *via* the Buphthalminæ, *Gymnarrhena*, *Centaurea* and the Centaureinæ. So close is the affinity that a microscopic investigation is necessary to distinguish some plants of *Gymnarrhena micrantha* (Inuleæ, Buphthalminæ) from *Centaurea furfuracea* (Cynareæ, Centaureinæ) and these two species grow in the same region.

The development of the Carduinæ from the Centaureinæ with the *Carduus-Cousinia* group as the basal plexus is clear, as is also the development of the Carlininæ and Echinopsidinæ from the Carduinæ. The evolution of these two sub-tribes along different lines from the same source is well shown in the secretory apparatus, the *Carduus* plexus gives the *Cirsium* line in the Carduinæ and the parallel *Carlina* line in the Carlininæ; the same plexus gives the Echinopsidinæ line and the parallel *Xeranthemum* line in the

Carlininæ. A slight degree of diphylesis is thus indicated for the Carlininæ and this is supported by other details, which suggest the *Atractylis-Carlina* plexus and *Xeranthemum* as the two basal groups (cp. Laviolle above, Chap. XII, D).

Considering the date of the origin of the Cynareæ, the facts are that this tribe is not represented with any certainty previous to the upper Miocene and that the *Arctium* type (Carduinæ) had then developed. If the above views on the phyletic of the tribe are correct this involves the previous existence of the *Carduus* type, which is also represented at the same horizon, and of the *Centaurea* type, which is not as yet reported fossil below the upper Pliocene. The time interval necessary for this development takes the origin of the Cynareæ back to the lower Miocene or Upper Oligocene. As the shrinking of the Central Sea reached its maximum about this time, the semi-desert condition of the eastern Mediterranean region would appear to have developed then. The connection between the origin of the Cynareæ and the ecological conditions in the place of origin has been discussed previously, and the synchronising of events in climatic evolution with events in plant evolution appears to be exemplified in the origin of the Cynareæ as well as in the origin of *Senecio*.

Mutisiæ. The basal group of the Mutisiæ is undoubtedly the Nassauviinæ and the basal genus is shown to be *Trixis* by the characters of the styles, stamens, pappus and other achenial hairs, receptacle and involucre. This is confirmed by the geographical distribution of the genus and sub-tribe and by the Senecionoid habit of many species of *Trixis*. The colour of the corolla in *Trixis* is also primitive and the distinguishing feature is the homogamous capitulum of bilabiate florets. Since the ray floret of *Senecio* and other radiate genera has been shown to be essentially bilabiate, and since it has also been shown, though with less certainty, that the number of rows of bilabiate florets, i.e., the amount of "doubling," depends on the food supply of the capitulum, the change from *Senecio* to *Trixis*, from the Senecionæ to the Mutisiæ, is evidently one which is largely dependent on ecological conditions.

In Chap. V, D, it was suggested that *Mutisia* gave rise to the rest of the Onoseridinæ and to the Gochnatiinæ, while *Onoseris*, as the other member of the basal plexus of the Onoseridinæ, gave the Gerberinæ. The evolution of these groups is further discussed in Chap. X. *Chuquiragua* is suggested as the basal genus of the

American Gochnatiinæ and the *Ainsliæa-Dicoma* group as the source of the Old World Gochnatiinæ. As *Ainsliæa* is more closely allied to *Mutisia* than *Dicoma*, that genus may be substituted for the double group.

Gerbera and *Chaptalia*, which are separated only by the abortion of the posterior lip of the ray florets in the latter and its presence in the former genus and by their geographical localities, form a very good basal plexus for the Gerberinæ. The differences between these two genera and *Onoseris* are of no more than specific rank in other genera, except for the type XII style of *Gerbera* and *Chaptalia* and the type IX style of *Onoseris*. A glance at Fig. 5 will show that the type IX style could be regarded as a type XIIa style in which the stigmatic papillæ had spread over the whole of the inner surface and in which the style branches had closed up. The former style would be the more primitive, but the difference is so slight that the evolution of the Gerberinæ from *Onoseris* is quite probable. These suggestions involve a slight change in Fig. 7 which would bring off the Gochnatiinæ from the Onoseridinæ instead of from the Gerberinæ.

The two genera of the Barnadesiinæ, *Barnadesia* and *Schlechtendahlia* with type 3 or type 4 stamens and type IX styles have probably arisen separately from distinct sources, and this sub-tribe is another example of polyphyly and convergent evolution. Until a detailed examination of their affinities has been made they can be regarded as a separate development, as shown in Fig. 7.

The separation of the Mutisieæ into two geographical groups furnishes some clue to the early history of the tribe. That the separation is geologically recent is proved by the affinity of *Gerbera* and *Chaptalia*. That the separation was due to the last Glacial Epoch is rendered probable by the recency of the event and by the fact that the Mutisieæ are tropical and subtropical plants. Such species, although they probably crossed the Alaska-Siberian bridge during the pre-glacial and interglacial warm periods, were unable to survive in the more northern latitudes during the period of glaciation and only a few primitive, i.e., physiologically undifferentiated, species, such as *Gerbera Anandria*, are even now becoming acclimatised to sub-arctic conditions.

The origin of *Trixis* is thus thrown back some considerable time to allow for the differentiation and dispersal of the higher types, such as *Gerbera*. Since the area occupied by the tribe is

considerably larger than that of the *Cynareæ* and since the differentiation of types within the tribe is greater than in the *Cynareæ*, a date antecedent to the origin of the latter tribe is indicated; taking into account the similarity in the areas occupied by the *Inulinæ* and by the Old World *Mutisiæ*, and the greater area of the whole of the *Mutisiæ*, the lower Oligocene is a probable date for the origin of the *Nassauviinæ*, with an extension into the Old World about middle Oligocene times.

Vernoniæ. The evolution of this tribe from the *Senecioninæ* via the *Liabinæ* is abundantly proved by most of the details of the florets and capitulum. The affinity between the *Liabinæ* and the *Vernoniæ* may be judged from the fact that *Gongrothamnus*, a genus of the *Liabinæ* according to Bentham, is Sect. IV of the genus *Vernonia* according to Hoffmann. The primitive genus, *Liabum*, of the *Liabinæ* is closely connected on the one hand with the *Senecioninæ* and on the other hand with *Vernonia*, the primitive genus of the *Vernoniæ*. The derivative position of the *Lychnophorinæ* is confirmed by most of the floral details and by the geographical distribution of the sub-tribes. The primitive genus is probably *Elephantopus*; the only character which raises any doubts of the primitive position of this genus is the form of the corolla, which sometimes has a posterior split.

The generic differentiation in the tribe is comparatively slight. Bentham (I, 7) remarks that the *Vernoniæ* "consists principally of one large genus with a number of smaller ones closely connected with it forming altogether one sub-tribe or generic group of a higher order." The distribution is entirely tropical or sub-tropical and the use of the Alaska-Siberian bridge by the tribe is not in any way indicated. These facts and the close affinity with the *Senecioninæ* point to a comparatively recent origin for the group, but the wide tropical distribution indicates an origin precedent to that of the *Calendulæ* or *Arctotideæ*. Taking all the data into consideration the date of the origin of the *Vernoniæ* seems to be about the middle Miocene; the place of origin is clearly the Brazilian region.

Astereæ. Various changes have been suggested in the evolution of the *Astereæ* as given in Fig. 7. The most important of these is the reversal of the *Homochrominæ* and *Heterochrominæ*, which has been completely vindicated by the analysis of other details than the styles and stamens, and also by a more critical examination of these structures.

The Homochrominæ is the basal sub-tribe and *Solidago* the primitive genus. An examination of any of the ordinary keys to the British flora, such as that in *Hayward's Botanist's Pocket Book* will show how closely allied are the three genera, *Senecio*, *Solidago* and *Inula*. The case of the Inulinæ is discussed above. The imbrication of the involucre bracts and the rigidity of the pappus hairs are apparently the best characters which can be found to distinguish *Solidago* from *Senecio*, and these apply only to the British species. The rigidity or silkiness of the pappus varies, especially in *Senecio*, while that same genus has exotic species in which the calyculus is so well developed that the involucre must be described as imbricate. The type VIII styles of *Solidago* are the real tribal distinguishing feature, but even this distinction is not absolute, since various species of *Senecio* show the type VIII and type VII styles.

The place of origin of the Homochrominæ is clearly somewhere about the borders of the Mexican and U.S. regions. This sub-tribe has in all probability given the Bellidinæ, while the Grangeinæ and Conyzinæ have probably come from the Heterochrominæ (see Chap. X, D), the Conyzinæ via *Erigeron*, which passes on the one hand into *Aster* and on the other into *Conyza*.

The transition from the Homochrominæ to the Heterochrominæ can be located in the region of origin of the former sub-tribe. The chief genera of the latter sub-tribe are *Aster*, *Erigeron*, *Olearia*, *Felicia* and *Celmisia*; of these *Olearia* and *Celmisia* are restricted to the Australian region, while *Felicia* is almost confined to South Africa. The other two genera are more or less cosmopolitan and are so very closely allied that the transitional species are comparatively numerous and the genera in these cases are distinguished only by the so-called indefinable characters of the taxonomist. On the other hand *Solidago* is "only distinguished technically from *Aster* and its immediate allies by the homochromous florets, the ray-florets, when present, being yellow, like the disk—a character in general of so little value that it cannot, in *Senecio* for instance, be admitted as of more than specific importance" (Bentham, I, 7).

The Baccharidinæ, which include only the large genus *Baccharis* and two very small genera, show affinities with the Heterochrominæ and especially with the Conyzinæ in styles and stamens (see Fig. 7), corolla-form, pappus, involucre, receptacle and phyllotaxis. The chief distinctions are the dioecious capitula

and the habit. The Baccharidinæ can, therefore, be regarded as a special American development of the African Conyzinæ type either from *Conyza* or more probably by parallel evolution from the *Erigeron* type of the Heterochrominæ.

The data available for the determination of the date of origin of the Astereæ include the occurrence of *Eupatorium* in the middle Pliocene of Europe. The origin of the Eupatorieæ from the Heterochrominæ may be considered proved, so that the origin of the Homochrominæ is thrown back a considerable time to allow for the wide dispersal and differentiation of the various types. The fossil record of authentic Astereæ is very meagre and does not extend beyond the Glacial Epoch. Several of the achenes from the lower Oligocene and upper Miocene are of the Asterean type. Taking into account the wide dispersal of not a few genera of the tribe and the wide dispersal also of the derivative Eupatorieæ, as well as the considerable differentiation of types in the Astereæ and Eupatorieæ, the date of origin for the Homochrominæ can scarcely be later than the middle Eocene, and might well be earlier still.

Eupatorieæ. The hypothesis of the origin of the Eupatorieæ from the Heterochrominæ has been more or less confirmed by all the characters of the group. The basal sub-tribe is the Ageratinæ and the basal group of this sub-tribe is the *Eupatorium-Mikania* plexus. The affinity of *Eupatorium* with the Heterochrominæ in styles, stamens, corolla colour, pappus, involucre, receptacle, and to a lesser degree the phyllotaxis, is distinct. The difference in the styles is the difference between type II and type VIIIa, and the chief distinction is in the complete absence of ray florets. Turning again to the above-mentioned key to the British flora we find that the discoid *Aster Linosyris* is distinguished from *Eupatorium* by the colour of the corolla and the shape of the leaves, characters which are in most cases of only specific rank.

The reduction in the complexity of the floral structures extends to the stamens in the Piqueriinæ (see Chap. II, E). The basal genus of this sub-tribe is *Adenostemma*, with its one wide spread species *A. viscosum*. The basal genus of the Adenostylinæ is probably the American genus *Brickellia*; *Adenostyles*, however, shows an approach to the *Cacalia* type of *Senecio* in habit and involucre (cp. Bentham, I, 7, p. 401). As *Adenostyles* is chiefly developed in the Eur-Asiatic region this case requires further investigation; the genus may be a development of the *Ligularia*

section of *Senecio*, which approaches the *Eupatorieæ*, particularly in the characters of the style.

The place of origin for all three sub-tribes of the *Eupatorieæ* is clearly the Mexican region.

In discussing the age of the *Eupatorieæ* Bentham (*loc. cit.*) showed more than his usual remarkable perspicacity. He considered that the *Eupatorieæ* "may be regarded as one large and natural essentially American group or genus in an extended sense of the term;" that they "must, therefore, either not be so ancient as some other groups of the *Compositæ*, or some other reason must have interfered with their early dispersion." Discussing the truncate anther-tips of the *Piqueriinæ* he says, "This remarkable deviation from the almost absolute uniformity of *Compositæ* is probably, therefore, of West American origin, and not ancient enough to have spread into other continents now severed from America."

The fossil evidence of the early history of the *Eupatorieæ* is interesting. The species of *Eupatorium* which now occupies the greatest area is identified in the fossil condition in Interglacial times, and other species are described from the upper and middle Pliocene. Considering these points and those indicated by Bentham, the date of origin of *Eupatorium* must be not later than the lower Pliocene. Taking into account the comparative development of the *Eupatorieæ* and the *Arctotideæ* (which is assigned above to the lower Pliocene) and the fact that *Eupatorium* had apparently arrived in Europe as early as the middle Pliocene, the most probable date of origin for the genus and tribe seems to be the middle Miocene.

The *Eupatorieæ* and *Vernoniæ* would on this hypothesis have arisen more or less at the same time. This would account for the similarity in sub-tribal and generic differentiation in these two tribes, as well as for the similarity in their geographical distribution (cp. Figs. 36-37).

Heliantheæ. Throughout the preceding chapters no reason has appeared for making any change in the phylaxis suggested for the *Heliantheæ* in Fig. 7. A more detailed analysis of the genera, however, suggests certain modifications. The *Verbesininæ* is clearly the primitive sub-tribe and *Spilanthes* is the most probable primitive genus for the sub-tribe (see Chap. X, C). In connection with the setiform aristæ of this genus it is interesting to note that Blake (159), discussing the few-membered, paleaceous pappus of *Hymenostephium*, says that it "is certainly not to be looked upon

as primitive." Although he does not say which type is to be looked upon as primitive, the derivative position of the paleaceous type agrees with the views expressed above and in Chap. V on the primitiveness of the setose type.

The Coreopsidinæ are very closely allied to the Verbesininæ and the primitive genus is probably *Coreopsis*, although the oligotypic genera *Guizotia* and *Microlecan* are even more closely allied to the parent group. As the centre of origin for all the sub-tribes of the Heliantheæ, except the Petrobiinæ, is clearly the Mexican region, and as the two above-mentioned genera are African, the affinity is evidently another case of convergent evolution. The intimate connection between *Bidens* and *Coreopsis* indicates that these genera have been contemporaneous almost from the origin of the sub-tribe.

The Galinsoginæ are closely connected with *Spilanthes* through *Calea*, the chief genus of the sub-tribe. which has type IV style, type 4 or type 5 stamens, and differs chiefly in the numerous scales of the pappus, which are, however, sometimes as few as four, and narrow, rigid, acuminate, approaching the setiform type of *Spilanthes*.

The Lagasceinæ and Petrobiinæ are two small, somewhat anomalous groups, which in the absence of a detailed investigation can be taken as coming from the Verbesininæ as in Fig. 7.

The Madiinæ, with the *Layia-Madia* group indicated as the primitive plexus, are more closely allied to the Galinsoginæ than is suggested in Fig. 7.

The Zinniinæ, especially *Zinnia*, is so closely connected with the lower Verbesininæ that it is impossible to give a precise source for the sub-tribe without more detailed investigation.

The Ambrosiinæ are more closely connected with the Melampodiinæ than with the Verbesininæ as suggested in Fig. 7. The affinity between *Iva* (Ambrosiinæ) and *Parthenice* (Melampodiinæ) is so close that there can be no doubt of the systematic position of the Ambrosiinæ in the Heliantheæ and also very little doubt, if any, of the origin of the sub-tribe from the Melampodiinæ via *Parthenium*, *Parthenice*, *Cyclachæna* (= Sect. I of *Iva* Hoffmann) and *Iva*.

The affinities of the Verbesininæ, Melampodiinæ and Milleriinæ are quite clear. Bentham (I, 7, p. 434) points out that the Melampodiinæ are "intermediate between Milleriæ and the great mass of the Helianthoidæ (Verbesinæ), differing from the former in the completely paleaceous receptacle, from the latter in the constant sterility and undivided styles of the disk-florets."

The transition from the Melampodiinæ to the Milleriinæ is effected according to the same author by the Milleriinean genera *Riencourtia*, *Desmanthodium* and *Clibadium*. As the last genus has since been shown by Blake (VII, 2) to belong to the Melampodiinæ the affinity is apparently closer than is suggested by the arrangement in Fig. 7, i.e. the Milleriinæ have been derived directly from the Melampodiinæ, not from the Coreopsidinæ on the same phyletic line.

Melampodium by its floral characters and distribution is indicated as the primitive genus of the Melampodiinæ. A comparative examination of the genera of the Coreopsidinæ and Verbesininæ shows that the differences between *Melampodium* and these genera are slight. Only the first seven genera of the Verbesininæ agree with *Melampodium* in having the outer achenes enclosed by the periclinial bracts. Of these seven only *Siegesbeckia* and *Enhydra* have some of the disc florets sterile, thus approaching the completely sterile condition of the disc florets in *Melampodium*. The involucre in *Enhydra* is rather special, consisting of two outer and two inner bracts, but that of *Siegesbeckia* is biseriate as in *Melampodium*; the former genus has often five outer or calycine members and the latter has four or five. Other affinities between these two genera can be traced. The type XIII style of *Melampodium* can be regarded as a closed type VII style and this type occurs in *Siegesbeckia*, where the branches are already short. In both genera the stamens are type 3, the ray-florets are uniseriate, the pappus and other achenial hairs are absent, the receptacular paleæ sometimes encircle the disc florets, the corolla colour is yellow, the cauline leaves are opposite and sometimes dentate. *Siegesbeckia* plants are annuals and so are some species of *Melampodium*. Both genera occur in the Mexican and Andine regions and extend to the Old World. The areas of the two genera are very similar but that of the older one, *Siegesbeckia*, is larger, since *Melampodium* extends in the Old World only into the tropical Asiatic region, while the weedy *S. orientalis* extends into all the Old World regions. The Melampodiinæ are, therefore, derived, not from the Coreopsidinæ as suggested in Fig. 7, but from the Verbesininæ via *Siegesbeckia* and *Melampodium*.

The date of the origin of the Heliantheæ is shown to be early by the common occurrence in Europe of the American genus *Bidens* in the upper Pliocene. That it is probably much earlier than this epoch is indicated by the Coreopsidean achene of *Carpolithus*

hyoseritifomis from the lower Eocene of America. The wide distribution of some of the higher types and the more extensive generic differentiation in the Heliantheæ than in the Astereæ renders it probable that the lower Eocene is the latest date which can be regarded as probable for the origin of the tribe. Taking all the data into account the origin of the Heliantheæ can be placed very soon after the origin of the family, and it is possible that the more primitive genera of the tribe originated in South America. *Spilanthes* shows a considerable Andine development as well as a centre of overlapping in South America. (See Fig. 39 and also the suggestion by Blake (159) that the South American section *Euaureæ* of *Viguiera* is the primitive one). Although the Heliantheæ probably arose in South America they undoubtedly attained their greatest development in the Mexican and U.S. regions, and the origin of most of the sub-tribes is probably to be located in these last two regions.

Heleniææ. Throughout this investigation affinities have been indicated for the Heleniææ with two tribes, the Heliantheæ (Galinsoginæ) and the Senecioneæ. With the possibilities of polyphyly and convergent evolution which have been discussed, the close connection of the Heleniææ with the Senecioneæ, which was recognised by Bentham, and the affinities which are also shown with the Anthemideæ and the Heliantheæ, the probability is considerable that this tribe is an artificial one, distinguished only technically from the Senecioneæ by the paleaceous pappus. If this view is correct the tribe requires reclassification on a more natural basis and it would serve no useful purpose to discuss the affinities of the sub-tribes at the present stage.

That the origin of most or all of the genera is comparatively recent is indicated by the restricted distribution and the comparatively slight generic differentiation within the tribe. The date of the origin of the oldest genera, such as *Pectis* and *Porophyllum* (Tagetinæ) *Flaveria* (Flaveriinæ) and *Jaumea* (Jaumeinæ) can scarcely be earlier than the upper Miocene.

CHAPTER XIV.

THE STORY OF THE COMPOSITÆ IN TIME AND SPACE.

THE conclusions arrived at in the preceding section are summarised in Fig. 79, p. 297. The geographical centre of origin of each tribe is indicated by a number corresponding to the table of regions on the left. The primitive genera are indicated in those cases where they are obvious without any detailed discussion of all the genera in the group. In some cases the centre of origin as given in Fig. 79 does not coincide with the main centre of concentration as given in Chap. X; this is because the probable primitive genus has its centre of origin in a region different from that of the chief development of the genera of the group. The change is made at this stage so that Fig. 79 may form the basis of future discussions and for that reason it should be as nearly a true representation of the history of the family as it is possible to attain without a detailed consideration of each one of the 23,000 species. The time of the origin of each sub-tribe, as deduced from the palæobotanical evidence and from the present development, generic and specific differentiation and area of the various groups, is also indicated.

An attempt will now be made, using Fig. 79 as a basis, to give that "coherent account of the evolution of the family" which, as mentioned in the Introduction, can be attained by the use of "the modern theories of heredity, evolution and geographical distribution." The writer's problem is to convey to the mind of the reader something of the activity and individuality which have been shown in the development of this immense family. A similar attempt was made in Chap. XI to picture the evolution of *Senecio*, but the cross-references given there interrupt the flow of the narrative and, in the present case, the reader is referred to all that precedes this last chapter for the proofs, the evidence for suggestions and the discussion of the various problems raised.

In the days immediately preceding the Cretaceous uplift on the west coast of South America, the Angiosperms had developed a multitude of forms which represented most of the larger families now existing. The forests of the Amazons to this day retain the very mixed character of this nursery of the Angiosperms: no one group was or is dominant, while the vegetative characters varied comparatively slightly owing to the similarity of conditions throughout a wide expanse of country. The inherent instability of this comparatively new plexus was the cause of the many mutations

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in the reproductive parts which differentiated the larger families. The arborescent habit of the ancestors of the Angiosperms was continued in the new group, so that there were only trees, shrubs and woody plants growing on trees, lianes and other climbers, in that particular region. Certain of the groups had already sent out colonisers which, especially the arborescent forms, had begun to make some headway, chiefly in the flat lands which formed the bulk of the earth's surface at that time. This period, in fact, was the Mesozoic Pre-differentiation Era of Guppy.

When the Cretaceous uplift raised the Andes well above the tree-limit a new habitat was produced, inaccessible to the trees and climbers as such, but offering a clear, unoccupied region to such of the climbers as were sufficiently plastic to develop into low-growing shrubs.

Among these plastic plants were the members of the *Siphonophyllus-Centropogon* group, which proceeded to colonise first the lower and then the higher slopes of the new mountain range. Under such altogether strange conditions many epharmonic variations took place and the Differentiation Era or Age of Compositæ (cp. Guppy) was initiated. The first form of Compositæ was a low-growing, woody, dwarf plant with the inflorescence and flowers of *Senecio*, as explained in Chap. XI.

The new form of fruit, with a dispersal mechanism eminently suited to the wide, windy, more or less barren, mountain regions, combined with the simplicity of the physiological constitution of the plant which was its inheritance from the Pre-differentiation Era, led to a very large development and wide dispersal of the *Senecio* form throughout the Andine region during the evening of the Cretaceous day. A similar form, which, however, may be of much more recent origin from the same plexus, is seen in *Lysipomia*, where the calyx persists in a clumsy, leafy form, so that this genus possesses no particular means of distribution and is still confined to the region of its origin.

Eocene Period.

Among the many forms developed by *Senecio* one of the earliest distinct types, *Gnaphalium*, with more complete aggregation of parts, was produced by the conditions near the snow-line. Another of the early types was the result of the re-invasion of the lower, more temperate regions by the now very definitely organised and aggressive *Senecio*. The annual and rhizomatous, perennial, herbaceous forms of *Senecio* probably developed in connection with

local, slightly sheltered conditions in the mountains and also with the short "summer" season. Such forms rendered possible the invasion of the open tracts in the lower regions and the *Spilanthes* type was the result.

The lower Eocene was now well advanced and *Senecio* had proceeded north to the Rockies, where the greater rainfall and less intense insolation rendered both the stunted, shrubby habit and the large-leaved xerophytic habit unnecessary. The usual *Senecio* of these regions was, therefore, of a herbaceous perennial type. The earliest progeny of the genus naturally accompanied the parent, *Gnaphalium* travelling along the higher mountain levels and *Spilanthes* along the foot-hills and alpine meadows.

The mountain habitat formed by the slowly rising Rockies was comparatively restricted and the successful invaders from the Andes extended their zone of occupation to the wooded regions of the plains. There the setose pappus would be of little use as a means of wind-despersal. Accordingly, the tendency to fusion of the setæ had more or less free play and the ten-awned type of fruit represented by *Carpolithus hyoseritifformis* was developed, the rest of the plant remaining very similar to the parent *Spilanthes*. Animal denizens of the forest would be much more efficient seed-dispersers than the gales which scarcely penetrated below the forest roof. The development of the free ends of the setæ into hooks, erect as in *Coreopsis* or recurved as in *Bidens*, was, therefore, a very successful experiment; so successful indeed that the latter of these experimental forms spread in time all over the surface of the earth.

Senecio travelled far and wide along the paths mapped out by the isolated hills and mountains, which by the end of the Eocene had appeared in most of the now mountainous regions of the world. The development of the different types would naturally be greatest nearest the Andine centre, where the numbers of individuals would also be greatest. The less arid conditions of the Rockies favoured a large development of the herbaceous forms. The lapse of time had given the tendency to elaboration of the style branches an opportunity to develop the elongated appendages characteristic of the *Astereæ*; the evolution of the flimbrillæ and alveoles of the receptacle and the aggregation of the cauline leaves to form a multiseriate calyculus had also been carried forward several stages. The most noteworthy result of these changes was the development of *Solidago* during the middle Eocene in the central region of North America. By that time the four main types of *Compositæ* had been initiated, *i.e.*, the *Senecioneæ*, *Inuleæ*, *Heliantheæ*, and *Astereæ*.

New conditions were required for further marked differentiation and these were attained when *Senecio* reached the Mediterranean region, by way of Alaska, Siberia and the Asiatic mountain ranges. The shrinkage of the Great Central Sea, which at one time stretched from the Gulf of Mexico to the Deccan, and the initial development of the Alps in upper Eocene times prepared a new land for *Senecio* to conquer. The low hills with abundance of marshland, and the sub-tropical climate combined to produce marshy woods and low-lying meadows in which the setose pappus was again of little use. Other experiments in fruit dispersal were, therefore, made here. Animal dispersal, especially by birds, was obtained by the reduction of the pappus to a ring or auricle, and the edible fruit was thus exposed to view. An occasional improvement was effected by the development of a mucilaginous pericarp, which would be very efficient in such a marshy environment. These changes, combined with a few slight and probably mutational changes in the styles and sexual arrangements within the capitulum, sufficed to produce the Anthemideæ as represented by *Chrysanthemum* and *Matricaria*.

Another method of getting rid of the superfluous pappus was tried with success; the pulvini of the setæ, which normally act only in dry air, having no opportunity of exercising their usual function, degenerated into regions of abscission, and the pappus became caducous. A preliminary attempt at raising the pappus was probably due to the fruit continuing growth under the predominantly moist climatic conditions. The initiation of both these experiments is seen in *Lactuca*, but the two methods became distinct in the progeny of that genus. The very rapid growth of these Cichoriaceous herbs was probably responsible for the re-development of latex which had been suppressed from the time when *Siphocampylus* first started to climb the Andes. The profound disturbance of the organism under a climate so different from that of the Andine home of *Senecio* was probably responsible for the mutation which produced the ligulate florets and also for the fact that the bulk of the Senecioneal colony in the Mediterranean region were transformed partly into Anthemideæ and partly into Cichorieæ. The origin of two more large groups is thus traced to the evolution of climate, particularly in the Mediterranean region during late Eocene times, combined with the arrival of the aggressively migrating *Senecio*.

About this time also the *Solidago* type underwent anthocyan changes in the corolla, possibly as the result of the decrease in the

insolation of the North American as compared with that of the Andine region, or possibly as the result of a mutation similar to that which produced the red sunflower. The result of these and other slighter changes was the origin of *Aster* from the *Solidago* type.

Oligocene Period.

While these events were occurring in the Mediterranean and North American regions, the ancestral home of *Senecio* was becoming rather crowded by its numerous progeny. The accompanying spread of the genus led, during the lower Oligocene, to another invasion of the *caatingas* among the Andine foothills near the sources of the Amazons. These regions were wooded but the altitude and soil conditions combined to produce well lighted, sunny woods with comparatively small trees, rather than the dense, umbrageous type of forest characteristic of the lower parts of the Amazons valley. Such conditions favoured the development of the herbaceous perennial type of *Senecio*, and as the tendency to economy in polliniferous tissue became effective tails were developed to the anthers. This economy was counter-balanced by an extravagance in the development of a bifid upper lip in the ray florets. These two changes, the former an example of orthogenesis, the latter an example of a mutation which can scarcely be called orthogenetic, together with some very slight changes which did not involve any change in general habit, resulted in the production of *Trixis*.

This habitat, it will be remembered, is that of the scandent Lobelioid ancestors of the Compositæ. It is not surprising, therefore, to find that these invaders from the mountains, both *Senecio* and *Trixis*, developed scandent forms. In the former the flower remained typical of the genus at least until the end of the Oligocene. In the latter, which was a comparatively new form not at that time quite stabilised, floral changes accompanied the change in habit. The barbellæ of the pappus setæ elongated to give a plumose type and the anther tails became somewhat longer; at the same time the supply of extra material for the inner lip of the corolla was cut down by the innate economy of the family. These changes, all of which are expressions of general orthogenetic tendencies in the family, together with slight anthocyan changes in the corolla, combined to originate the genus *Mutisia* during the middle Oligocene.

By the end of the lower Oligocene all but the more restricted groups of the Compositæ had been initiated, so that the considerable variety in the *Cypselites* of that period, even in the Mediterranean region, is what might be expected.

During the middle Oligocene a considerable amount of differentiation took place, chiefly along the lines already laid down. Thus *Inula* was developed in the Mediterranean region by a series of orthogenetic changes all of which had already been initiated in *Senecio*. These changes included the spreading of the stigmatic papillæ all over the inner surfaces of the style branches, the elongation of the anther tails, the greater aggregation of the cauline leaves into the calyculus, and the increased development of bilabiate florets. This last change was probably due to the moist climate, where food material was abundant both for the greater vegetative growth shown by *Inula* and for the extra floral material required to produce numerous rows of bilabiate corollas. In the Mediterranean also, the same moist environment led to a development of the beaked achene with which *Lactuca* had been experimenting at an earlier date and the *Scorzonera* group was originated.

Events were meanwhile progressing in the Mexican region, where considerable geological changes were occurring. Similar conditions to those of the Mediterranean prevailed for a time and *Erigeron* was developed from *Aster* by an increased outlay in bilabiate corollas and a decrease in the number of protective involucre leaves, but, as the western end of the Great Central Sea continued drying up, the climate, at least locally, became much drier and a proportion of the *Erigerons* began to find conditions less favourable. The bilabiate florets were therefore reduced to filiform female florets and at the same time the protective action of more aggregated cauline leaves was required. *Erigeron* in these local dry regions thus became *Conyza*.

Before this time the moist conditions of the wooded parts of the Mexican region had induced *Spilanthes* to reduce the protective calyculus to a few leaves, and in the absence of opportunities for wind-dispersal the pappus and other achenial hairs ceased to be developed. Other changes had led to the production of a number of genera now classed as Verbesininzæ, but these particular developments produced *Siegesbeckia*. Continued existence under such favourable conditions gave the innate economy an opportunity to act by sterilising a number of the disc florets, thus reducing the number of fruits produced by each capitulum. This economy,

initiated by *Siegesbeckia*, was carried further until all the disc florets were sterile; then the style branches remained permanently closed, since the style survived only as a pollen presenter, and *Melampodium* came into being about the time of the middle Oligocene.

Meanwhile, further south, among the headwaters of the Amazons, *Mutisia* was being developed from *Trixis* by floral changes accompanying a recovery of the ancestral scandent habit as described above. The *Mutisia* type repeated the travels of its grand-parent *Senecio* and re-ascended the Andes, undergoing the changes necessary for existence on the more arid and windy mountain slopes. Food material for the capitulum being scarcer, the ray florets became reduced or sometimes ceased to be developed; the pappus regained its wind-dispersal function and was developed to a greater extent. In addition the scapigerous form was taken in the more barren regions where it was necessary. During this interesting journey *Mutisia*, in fact, became *Onoseris*.

Having regained an efficient wind-dispersal mechanism, the *Onoseris* type spread quickly. By a few slight changes, including the abortion of the inner lip of the corolla in the outer row of florets, which was quite natural under the unfavourable conditions of the Andine habitat, *Chaptalia* was evolved. The pappus being retained in an efficient condition, the mountain path north along the Rockies, across the Alaska-Siberian bridge and south along the mountains of Asia, was open for *Chaptalia*. This migration took place in the upper Oligocene and on reaching the plains of China the genus suffered the natural changes on regaining a mesophytic habitat. Increased food supply led to a redevelopment of the aborted inner lip of the outer corollas and a reduction in the number of protective calyculine leaves; *Chaptalia* in this way became *Gerbera* on crossing the Alaska-Siberian bridge.

The end of the Oligocene saw the initiation of a number of subsidiary lines of evolution, the most important of which was again connected with important geological events. The Mediterranean end of the Central Sea was undergoing considerable shrinkage, and this led to the development of spines in the *Inula* group. At the same time mutational changes developed the flimbrillæ of the receptacle into deeply lacerate alveoles, which surrounded the young fruits and to a certain extent prevented the pappus from exercising its normal function. The pappus setæ, therefore, fused in various ways and the Buphthalmiæ originated.

The shrinkage of the Central Sea continuing into the lower Miocene, a strongly insolated, semi-desert region was produced at

the eastern end of the Mediterranean, of which the dwarfed, reduced, spinescent *Gymnarrhena* was a natural inhabitant. The progressive elaboration of the style branches included the formation of the ring of hairs characteristic of the *Cynareæ* and the orthogenetic economy in polliniferous tissue led to the further elaboration of the anther tails. By an elongation of the achene and a reduction in the length of the receptacular setæ the pappus was again freed and *Centaurea* was produced. Being economical and easily dispersed by wind this type multiplied and spread to occupy the new habitat.

About the same time (end of the Oligocene and beginning of the Miocene) another of the periodical invasions of the Amazonian headwaters took place. Two mountain tribes took part in this invasion and the new environment of moist woods and *caatingas* had the same effect in both cases. The pappus was again rendered of little use and as a consequence became more or less atrophied by fusion. This change was most pronounced in the *Spilanthes* coterie and the *Calea* (Galinsoginæ) type was the result. The numerous progeny of the Andine *Senecios* were not so susceptible, and the fusion of pappus hairs was more or less confined to the outer rows; the style branches in this case, however, underwent considerable elongation and *Liabum* was the result. This genus afterwards re-ascended the Andes, undergoing the usual changes, becoming dwarfed and uncapitulate.

A neighbouring region, the Chilian part of the Andes, was invaded more or less simultaneously by *Mutisia* and its fellow genera from the foot-hills. This regaining of a region where the conditions rendered the food-supply of the capitulum rather problematical led to the complete suppression of the large corollas of the ray florets. At the same time the plumose pappus was once again in a position to exercise its natural efficiency and reduction in the number of fruits was possible. This was affected by the sterilisation of some or all of the florets of the capitulum and *Chuquiragua* came into existence.

Just as its cousin, or rather niece, *Chaptalia* raced along the mountain ranges on regaining an efficient pappus in a suitable environment, so did *Chuquiragua*. Like *Chaptalia* also, this new genus was transformed on crossing the Alaska-Siberian bridge by an increase in the corolla material, which was rendered possible by the mesophytic conditions of the upland plains of China. *Ainslia* is the name now giving to the transformed *Chuquiragua*. This

Ainslia type reached South Africa at a much later date (lower Pliocene) by means of a greater development of the pappus which made migration easier. During the journey it underwent a few other slight changes and became *Dicoma*.

To the north, in the Mexican region, the end of the Oligocene saw a descent from the mountains by the progeny of *Gnaphalium*. Such a migration to the moist wooded plains rendered the closely aggregated capitula of that genus unnecessary. Larger and less densely involucrate heads were developed, with some rounding off of the tips of the style branches, and a weedy habit was acquired. The result was *Pluchea*, another wanderer, which spread and developed largely on the other side of the Pacific.

Miocene Period.

Beyond a larger development of the *Cynareæ*, with the initiation of the *Carduus* type, in response to the continued evolution of the semi-desert area of the eastern Mediterranean region, the lower Miocene was comparatively uneventful. The only other events were confined to the Mexican region.

Gnaphalium again descended from the mountains, this time into the Californian valleys and, undergoing changes similar to those which originated *Pluchea* in a similar environment, it became *Filago*. This type, which like *Pluchea* spread to Asia, finally became well-developed in the Mediterranean and other regions lying on the path of migration.

In the Mexican region also, about the same time, the descendants of *Spilanthes* having reverted to their distant Lobelioid ancestors in producing receptacular bracts, again came into line with the rest of the *Compositæ* by omitting these accessory structures. Continued existence in the favourable mesophytic environment of the Mexican woods rendered the numerous involucreal leaves of those forms unnecessary and the result of these two changes was the initiation of the *Layia-Madia* group,

The middle Miocene, a geologically active period, was more eventful for the *Compositæ*. The orthogenetic elongation of the appendages of the style branches continued in the *Aster* plexus and the production in the open Brazilian woods of forms which, with the abundant food supply, produced dense masses of capitula had an interesting result. The crowding of the heads gave little room for ray florets and, the food supply of the dense inflorescence being limited by the conductivity of the peduncle, each capitulum would get a distinctly limited supply. These factors led to the

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suppression of the ray florets and the discoid *Eupatorium* was produced. A very similar development occurred in the *Liabum* group of the same region and *Vernonia*, which is very similar to *Eupatorium* in general form, was evolved. Both these genera spread across the Pacific archipelago during the succeeding periods.

The tendency to economise in fruit production was more or less general in these favourable regions at the foot of the Andes and it became very marked in some of the Brazilian Asters. Some of the capitula became completely sterile. Thus *Baccharis* originated, and by travelling up and along the Andes reached such a diversity of habitats that it gave rise to a very varied group of species.

In the Mexican region a considerable differentiation occurred, which was probably connected with the geological activity during the middle Miocene in and around what is now the Caribbean Sea. By changes in the colour of the ray florets in the Golden-rod tribe, similar to those which produced the Asters, combined with the always recurring suppression of the pappus, the Bellidinæ originated.

The tendency to reduction in the number of fruits produced by each capitulum, which had become well developed in the *Melampodium* plexus, was carried still further: the capitulum was reduced to a few flowers; at the same time the large anterior lip of the ray florets became reduced and *Clibadium* (Milleriinæ) was developed. The same two tendencies were carried to extremes along another line in the same plexus. *Parthenium*, losing the aristæ of the pappus and reducing the corolla of the female ray florets, became *Parthenice*. A still further reduction of the rays resulted in the genus *Iva*, in which the tendency to unisexuality of the flowers became so strong that unisexual capitula were developed in some of the other Ambrosiinæ. These series, the Milleriinæ and Ambrosiinæ, represent the working out to the last possible stage of orthogenetic lines commenced under the influence of the success of the capitulum as a seed-producing arrangement, together with the reduction in available food material resulting from the gradual drying up of the originally mesophytic environment as the shrinking of the Central Sea continued. In the mesophytic wooded localities which were left the *Spilanthes* group continued to thrive, and in some rather unsuccessful forms the awned pappus of the ray florets was lost by the mutation, common throughout the family, which resulted in the suppression of the achenial hairs and pappus.

Conditions being favourable these forms continued to exist, and, requiring something to replace the lost pappus, developed a substitute by rendering the corolla of the ray florets persistent. When the disc florets were fertile the awns were present or, if the loss mutation extended to all the flowers in the capitulum, tuberculations of the pericarp in the achenes of the disc were sometimes developed for dispersal purposes to replace the lost structures. These cases and the original development of the achenial hairs into a pappus are examples of the general rule that lost structures are not re-developed but are replaced by something similar developed from parts which are still present.

The other end of the Central Sea in the Mediterranean region was also active geologically during the middle Miocene. The continued evolution of the semi-desert region, with dryness and strong insolation as predominant characteristics, produced the spiny group (Scolyminæ) of the Cichoriæ. The changes in climate resulting from the alternating sinkings and uprisings of considerable stretches of the land surface were doubtless responsible for a considerable proportion of the diversity of forms produced in the Cichoriæ at this time.

One of the most interesting events of the middle Miocene was the origin of *Helichrysum* from the *Gnaphalium* line in South Africa. *Senecio* and *Gnaphalium* had by that time become established in this region, and finding the climate in these similar latitudes rather like that of their Andine home, as far as aridity, insolation, etc. were concerned, these two genera multiplied abundantly. *Gnaphalium*, more accustomed to living near the snow-line, yielded earlier than *Senecio* to the difference in altitude, and *Helichrysum* was produced. This genus was so suited to the conditions on account of its epharmonic origin that its numbers soon exceeded in a very marked degree those of its parent.

Probably on account of its lower physiological differentiation *Senecio* was slower in yielding, but in the succeeding period, the upper Miocene, it gave *Ursinia* by the changes which usually resulted from the attainment of a more favourable environment, where food material was abundant and wind-dispersal rather uncertain. The ray florets became neuter and the reduction in the number of fruits *per* capitulum was carried further by the sterilisation of the inner disc florets. At the same time fusion of the pappus setæ was accompanied by a development of the flmbrillæ of the receptacle to form flat setæ.

As time went on this new genus spread to the arid, semi-desert regions which were increasing in South Africa in the evening of the Miocene day; the dryness and strong insolation had the same result as they had at an earlier date in the Mediterranean region. The type became spinescent (*Berkheya*); reduction and aggregation continuing, as they did again later to produce *Echinops* among the thistles, the dense glomerules of the spinescent *Gundelia* and *Platycarpha* originated.

In addition to the origin of *Ursinia* the upper Miocene in South Africa saw the origin of the *Athrixia* line. The *Inula* group was by this time well represented in South Africa and a reduction in the corolla of the ray florets occurred, similar to that which had previously taken place in the similarly arid part of the Mediterranean region. This with other very slight changes gave the *Athrixia* line. On account of the continued drying up of the region, which produced a distinctly xerophytic habitat, the flat or slightly recurved leaves of *Athrixia* became much reduced and practically ericoid. The semi-shrubby habit changed at the same time into the typical xeromorphic shrubby habit. These conditions also led to a reduced or depauperate condition in the capitulum: very few flowers were developed in each head and this led to the usual aggregation. By these epharmonic adaptations *Relhania* and its congeners were originated.

Helichrysum by this time was well developed in South Africa and the xerophytic conditions had almost the same effects on this genus as they had on *Athrixia*. So much so that epharmonosis, in this case as in many others, led to convergent evolution, and the present systematic group *Relhaniinæ* includes both *Relhania* and *Metalasia*, which latter was the product of the second series of epharmonic variations.

A neighbouring event of this time was the origin of the *Grangeinæ* in tropical Africa. The *Asters* and *Erigerons* had followed *Senecio* along the lower levels of the mountains and on attaining the very favourable conditions yielded by the tropical African scrub underwent the usual reductions. The pappus first became reduced or caducous and then disappeared completely. At the same time the tendency to reduction of the rays, which was so well developed in the *Aster* plexus resulted in reduced ray florets.

Meanwhile the *Senecioneæ* in Mexico were again being affected by the mesophytic conditions which had previously led to the fusion of the pappus setæ in the origin of the *Galinsoginæ*, *Madiinæ* and *Liabinæ* near the beginning of the Miocene. In this case the

Heleniæ were originated. In all four cases a tendency to lateral fusion of the pappus hairs was present, and similar climatic and other ecological conditions are indicated by other data.

About the same time the tendency to reduction in the number of fruits, which is seen in the *Melampodium* line, became effective in the ancestral plexus of that genus and the one-flowered capitulum of *Lagascea* was developed in the Mexican region. In the northern sub-arctic regions of Asia the cold and other adverse conditions, including the short vegetative season, induced some of the Senecioninæ to assume the geophilous habit of *Petasites*.

Pliocene Period.

Events in the lower Pliocene occurred chiefly in the Old World and notably in South Africa. The above-mentioned origin of the *Metalasia*, *Relhania* and *Berkheya* groups and of the Tarchonanthinæ took place then. In addition those Senecioninæ in South Africa which were fortunate enough to have occupied the moist valleys found a reduction in fruit-number possible and the disc florets became sterile. As usual such conditions resulted in the reduction or complete suppression of the pappus, which was replaced in this case by bent apical beaks, tuberculations, and other structures suitable for animal dispersal. In this way the Calendulæ were developed.

Differentiation in the Mediterranean region was active chiefly in the Cynareæ as far as sub-tribes were concerned; the two groups of the Carlininæ and the Echinopsidinæ with aggregated, few-flowered capitula are probably the result of the working out to the furthest limits of efficiency of the two tendencies, aggregation and reduction. A large development of the Carduinæ is also suggested.

Reduction and aggregation were nearing the limits of efficiency in other tribes also and similar "end-products" can be traced in other geographical regions. Within the limits of efficiency but showing reduction came the Adenostylinæ via *Brickellia*, but in the same *Eupatorium* plexus the limits were passed in the Piqueriinæ which, originating in *Adenostemma*, remained as a consequence of their inefficiency a small, restricted group. These were Brazilian events and in the same region a parallel development occurred in the Vernoniæ, where the few-flowered, aggregated capitula of the Lychnophorinæ were developed in *Elephantopus*. Another very similar development occurred in the origin of the reduced, dioecious and geographically restricted Petrobiinæ in the Chilean region.

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By the time the middle Pliocene was reached most of the sub-tribes of the Compositæ had been differentiated and events occurred only in rather outlying regions. In Australia the *Helichrysum* line developed the same "end product" as the above groups in the reduced, few-flowered, aggregated capitula of the Angianthinæ. In South Africa the main stock of the family, the Senecioninæ, retaining its vitality to the last, gave off the Othonninæ by the fusion of the periclinal bracts. The only later sub-tribe to arise was the small group Gundeliinæ, another few-flowered, aggregated "end-product," which as mentioned above was produced in the same region from the *Berkheya* line in the upper Pliocene.

The upper Pliocene and the succeeding geological period were characterised by generic, specific and varietal differentiation rather than by the origin of larger groups. This is probably due to the short period of time which has elapsed since the middle Pliocene and, perhaps even in a greater degree, to the more settled climatic conditions of the earth as a whole.

It will be seen that a few fundamental tendencies or orthogenetic lines, largely if not entirely due to epharmonic variation, can be traced throughout the various tribes in their wanderings over the surface of the earth during the Tertiary evolution of climate. Little else is required to account for the main variations in form and physiology of the Compositæ and that little can be supplied by mutational phenomena such as we are accustomed to at the present time.

This is the story of the Compositæ in time and space and it is hoped that what has been lost in scientific accuracy has been regained to some extent in the coherence of the narrative. In any case the strictly scientific synantherologist is referred for facts to the preceding chapters and he can neglect and forget this attempt to bring a real, living picture of the origin and development of the Compositæ before the mind of the ordinary student.

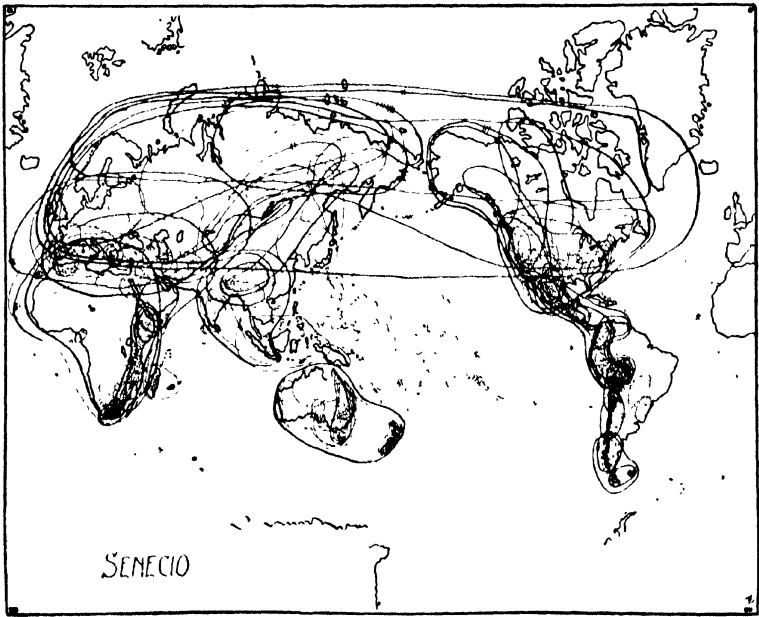


FIG. 29.

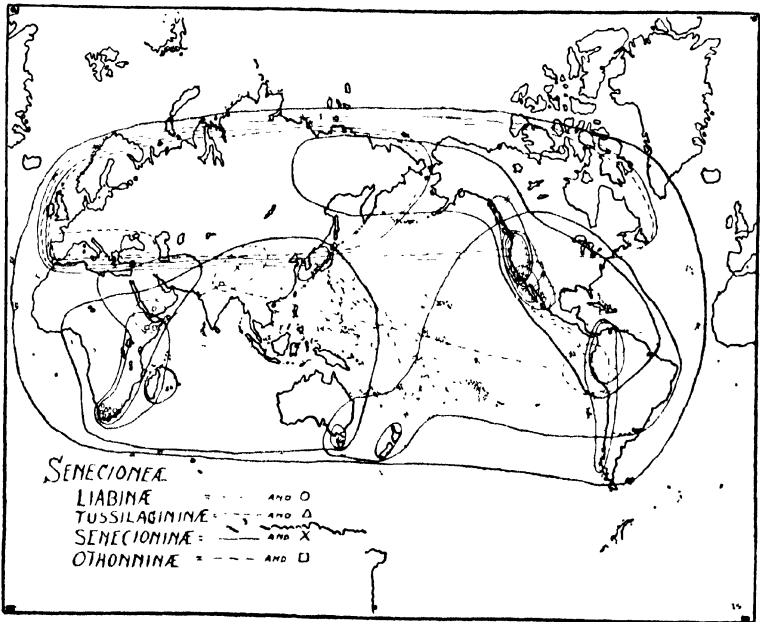


FIG. 30.

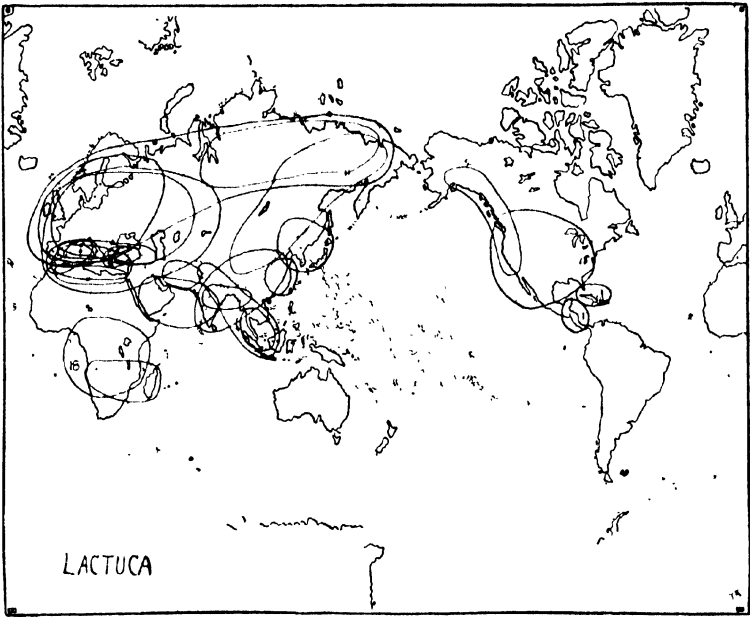


FIG. 31.

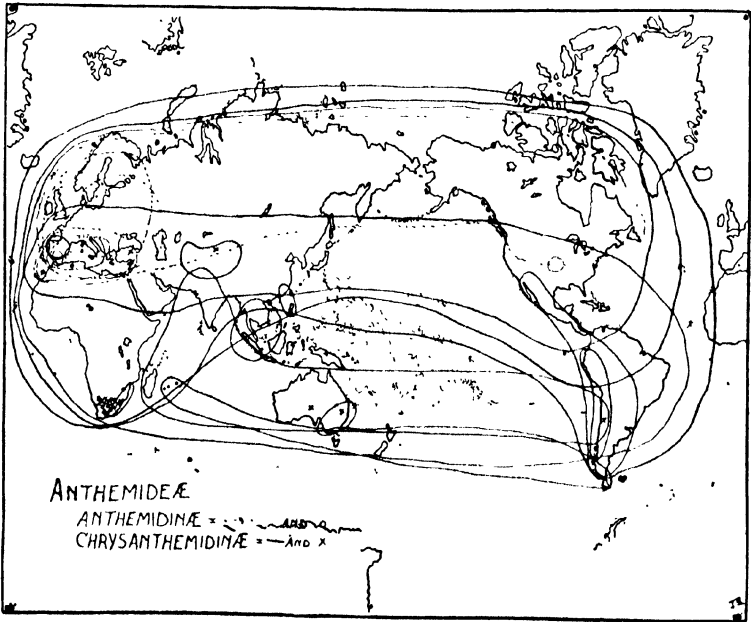


FIG. 32.

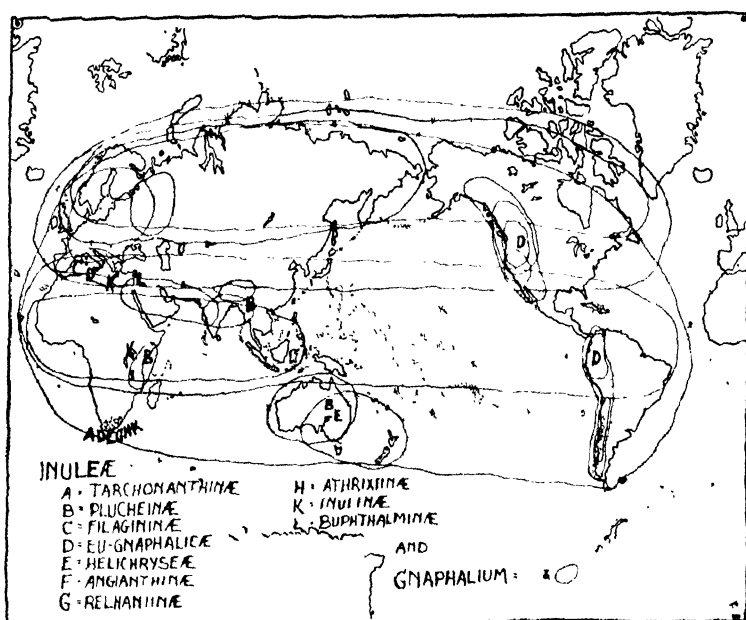


FIG. 33.

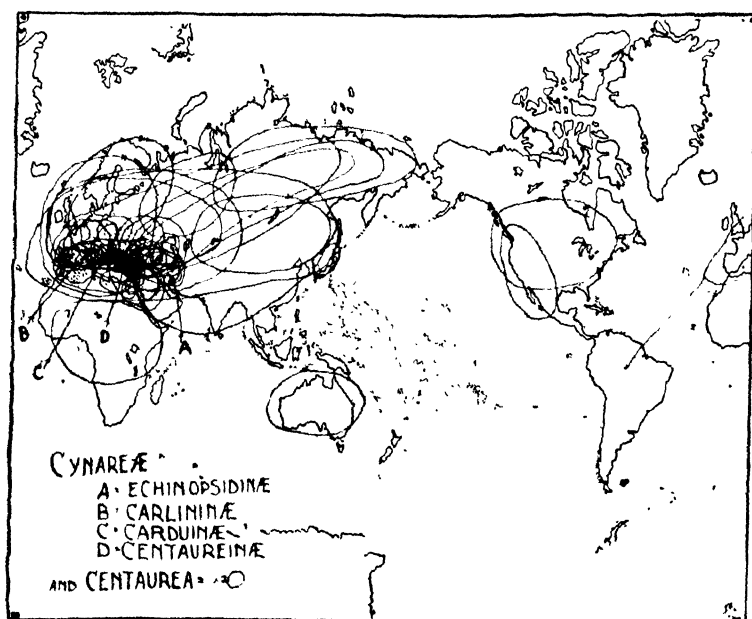


FIG. 34.

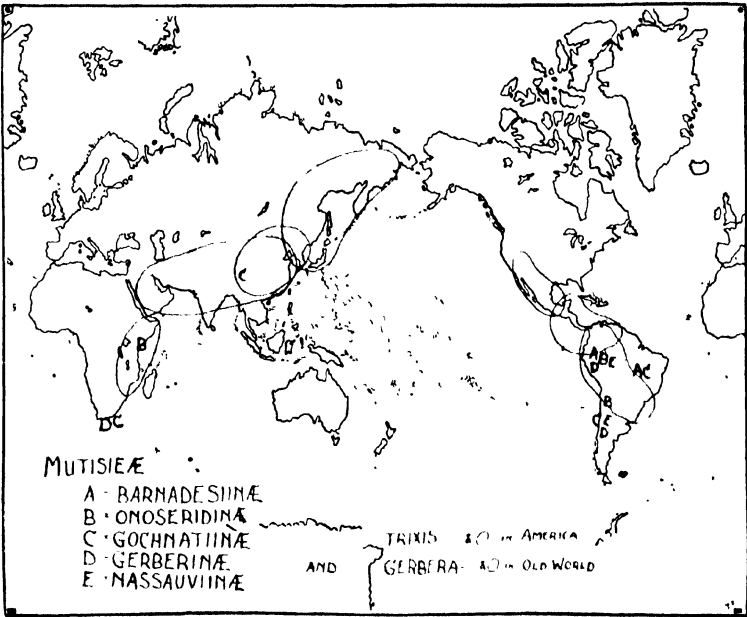


FIG. 35.

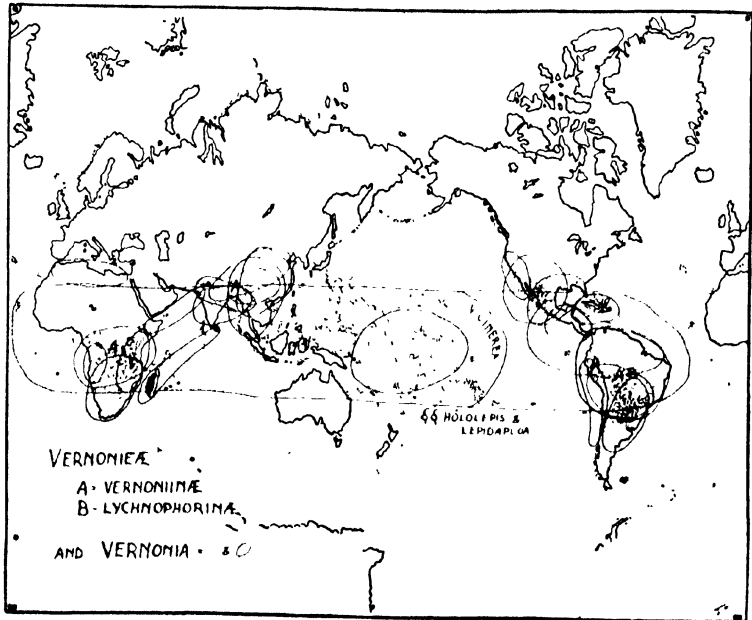


FIG. 36.

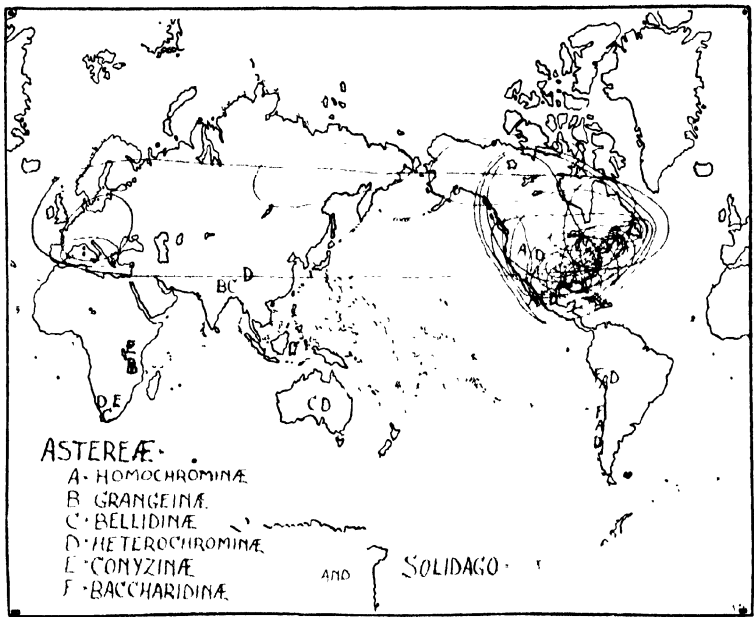


FIG. 37.

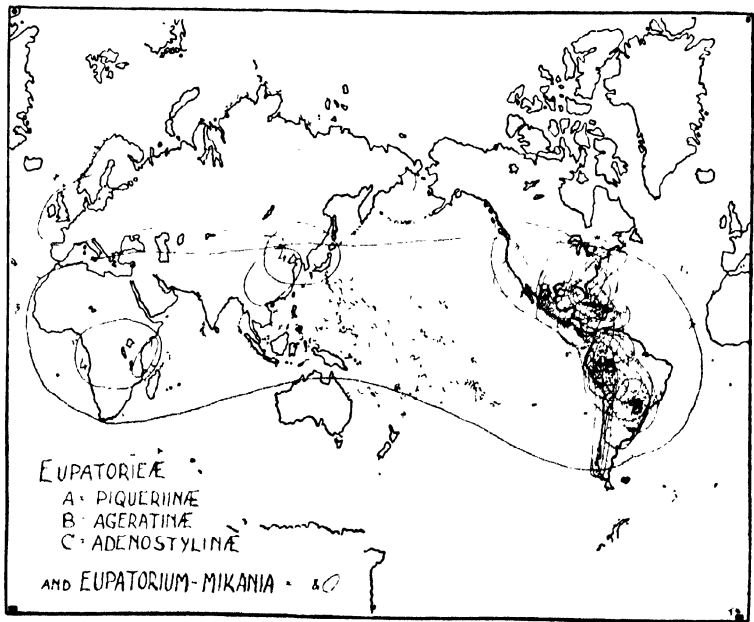


FIG. 38.

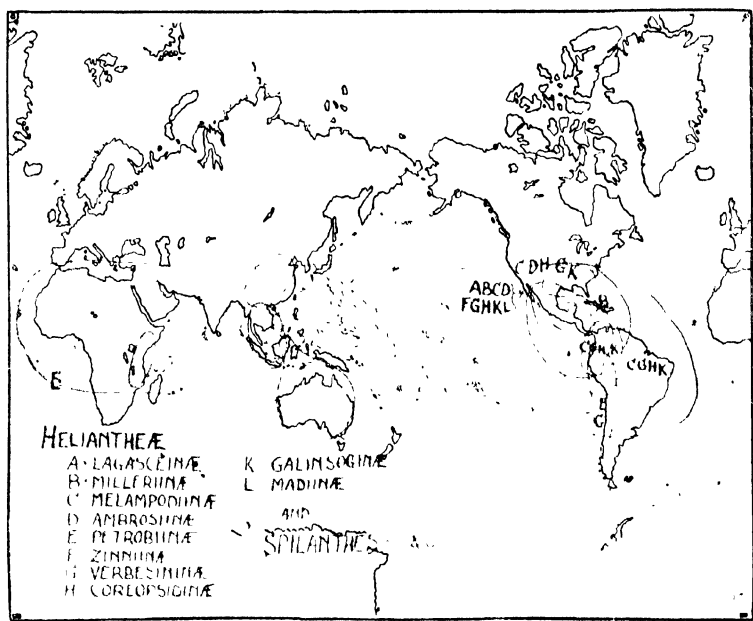


FIG. 39.

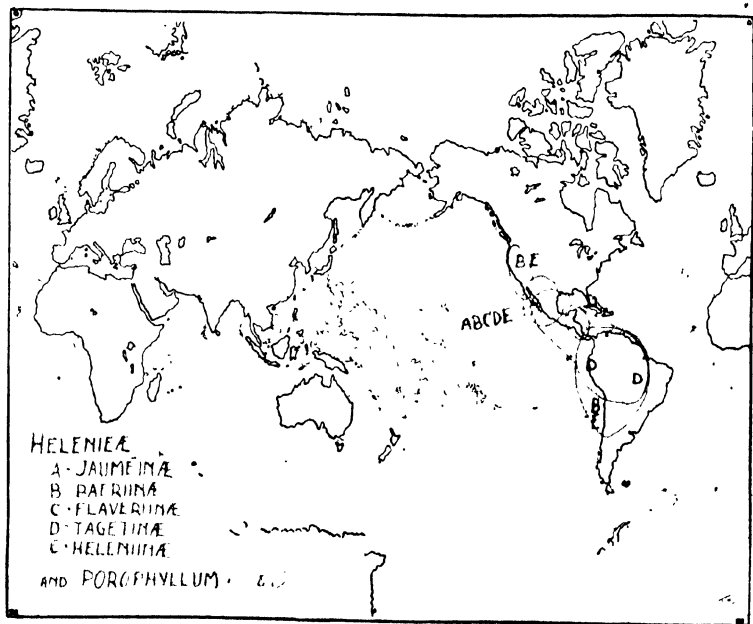


FIG. 40.

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